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THE BIOLOGY OF THE GARDEN CENTIPEDE, SCUTIGERELLA IMMACULATA[1,2]

A. E. MICHELBACHER[3]

INTRODUCTION

AN ATTEMPT HAS BEEN MADE in this study, not only to extend the knowledge concerning the garden centipede, *Scutigerella immaculata* (Newp.), but also to bring together much of the literature pertaining to it. The entire field is so extensive that it has not been possible to make a complete study of it. For this reason some of the material given has been obtained wholly from the literature. The fields most thoroughly studied are those which deal with the biological aspects.

Many of the activities of the garden centipede have never been investigated thoroughly, and since the organism is a serious economic pest, it seemed probable that a better understanding of its biology might aid in directing control measures.

During the present investigation the garden centipede has been studied under a great variety of conditions, including those of the laboratory, field, and greenhouse. Most of the field studies were confined to the low, rich, delta lands of the lower Sacramento River (fig. 1). Conditions over much of this area appear to be ideal for all the requirements of this animal. The Division of Soil Technology of the University of California characterizes the delta area as follows: it is low and flat and, for the most part, divided naturally into rather large islands surrounded by high levees which prevent them from being flooded. Most of this land is close to sea level, ranging from less than 10 feet above to 15 feet below sea level. In nearly all cases the land is below the level of the sur-

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[2] Presented as a thesis to the Graduate Division of the University of California, May, 1935, in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

[3] Junior Entomologist in the Experiment Station, Division of Entomology and Parasitology, Berkeley, California.

rounding water. The soils throughout most of this region are highly organic (10 to 90 per cent organic matter) and finely textured, the mineral soils having a high content of silt and clay. The soils naturally have a good structure and under proper farming methods are of good tilth. In some localities a second type of soil consisting of stream sediment is found, usually near the levees. This is of recent deposition and contains less than 10 per cent organic matter.

Naturally the soils are saturated with water and poorly drained, but under farming conditions they are relatively well drained by pumping

Fig. 1.—A view in the Sacramento River Delta showing the vast expanse of level country. Asparagus fields are seen in the foreground.

which lowers the water table to at least 2 feet below the surface. Even under these conditions the water content of the soils is high since their water-retaining capacities are great.

The entire area is devoted principally to the production of such field crops as asparagus, beans, sugar beets, and alfalfa, although deciduous fruits are grown on the higher ground near the levees.

Most of the life-history studies were conducted in the laboratory, and all work, unless otherwise noted, was done at room temperature, which averages very close to 21° C. Greenhouse studies were largely made in commercial plants where ample opportunities were afforded for the study of life history, plant injury, and artificial control.

HISTORICAL REVIEW

The class Symphyla has held the interest of many naturalists since about the middle of the eighteenth century. Numerous articles have been published which deal with its members. All the early workers were concerned principally with taxonomy, anatomy, and phylogenetic relationships of this group. While many of the later papers still deal with these subjects, there are some which consider the economic aspects, and several which are ecological in nature.

There are over two hundred papers on Symphyla. Some of these treat the class or some of its members in great detail, while others merely mention it in relation to other organisms or in faunal lists. Since the literature has been reviewed in numerous articles, it will be considered only briefly here, although in the text it is treated more fully in relation to points of interest in this investigation. Some of the papers which contain reviews of merit are: Latzel (1884*b*),[4] Grassi (1886), Schmidt (1895*a*), Haase (1889), Packard (1898), Hansen (1903*a*), Woodworth (1905*a*), Williams (1907*a*), Wymore (1924*a*), Attems (1926), Friedel (1928), Filinger (1931*a*), and Verhoeff (1933–34). The last-named author covers the subject most thoroughly.

The first species of Symphyla was described by Scopoli in 1763 as *Scolopendra nivea.* The fact that he described it as a *Scolopendra,* a genus of true centipede, gives evidence that he little realized that the organism possessed characters so distinct that eventually it would be placed in a class by itself. In 1839 Gervais named the second species, which he collected near Paris, *Scolopendrella notocantha.* Newport in 1845 named the third species *Scolopendrella immaculata* from specimens collected near London. Gervais (1847) placed his genus *Scolopendrella* in the Geophilidae. He gave a description of *Scolopendrella notocantha* and stated why he did not place it with *Geophilus,* although the first specimens he collected he thought were the young of some member of this group. Menge (1851) pointed out that *Scolopendrella* should not be classified with *Lithobius* or *Geophilus,* but, since it was more nearly like *Campodea* in characters and life habits, it should be considered as a transitional genus or family between Lepismidae and Scolopendridae. He also was the first to study the anatomy of the garden centipede, *Scutigerella immaculata* (Newp.), and did a creditable piece of work, with two exceptions. He thought that the organism possessed 4 Malpighian tubes instead of 2, the number found by later investigators,

[4] See "Literature Cited" for complete data on citations, which are referred to in the text by author and date of publication.

and was of the opinion that the genital opening was situated at the posterior end of the body instead of just anterior to the fourth pair of legs.

Rosicky (1876) placed *Scutigerella immaculata* (Newp.) under the order Chilopoda. In 1880 Ryder created a new order to include this interesting group, since his studies indicated as much affinity with insects as with myriapods. He named the order "Symphyla in reference to the singular combination of myriapodous, insectean, and thysanurous characters which it presents." Latzel (1884*a*) was of the same opinion. In 1881 Ryder further stated that *Scolopendrella* should be separated from the myriapods, and in 1882 he erected the second genus *Scutigerella* of which the Newport species became the type.

Probably the first note on Symphyla in America was that by Packard (1873) in which he described *Scolopendrella americana* sp. nov. (he later considered this as a synonym of *Scutigerella immaculata*) and remarked that it might be regarded as a connecting link between the Thysanura and the Myriapoda. After his study of *Scolopendrella*, he concluded (1881) that most of its characters were thysanuran-like, and that Symphyla should be included as suborder of the Thysanura. In 1883 he stated that later studies confirmed his previous opinion, and in 1898 he still held, after reviewing the literature, that *Scolopendrella* was much more closely related to the insects than to the myriapods. In 1903, however, he stated that his original idea that it was a thysanuran was a mistaken one and that Symphyla evidently formed a group by itself.

Wood-Mason (1883) reached the conclusion that *Scolopendrella* was a myriapod and that it was more closely related to Chilognatha than Chilopoda.

In 1886 Grassi published his very complete work in which he discussed habitat, systematics, anatomy, the various systems, and the relationship of the symphylans to other arthropods. He also added a new species, *Scolopendrella isabellae*.

Haase (1886*a*) stated that the myriapods and insects were closely related and sought to derive the Myriapoda, as well as the Apterygota, from a type related to *Scolopendrella*. In 1889 he reviewed the literature and made an extensive study of the abdominal appendages of insects with special reference to the myriapods. He gave a detailed description of the parapods and the ventral, or coxal, sacs, including their position, structure, function, and phylogenetic significance. In 1890 Graber pointed out that the abdominal appendages of *Scolopendrella* appeared similar to those of *Campodea*, *Japyx*, and *Machilis*. This similarity was also observed by numerous other workers.

Pocock (1893) remarked that no one who compares the *Scolopen-*

drella with a chilopod on the one hand and with a thysanurous hexapod on the other can avoid being struck by the fact that the differential characters between insects and the centipedes are, to a large extent, bridged over, and that *Scolopendrella* must consequently be regarded as the living form that comes nearest to the hypothetical ancestor of these two great divisions of the tracheate Arthropoda. He used the position of the generative organ in his classification in separating the various classes into groups. Since he thought that the generative organ in Symphyla was located at the posterior end of the body, he placed it with the Chilopoda and Hexapoda, whereas, according to his means of division, it should be placed among the Diplopoda and Pauropoda, because the sexual opening is near the anterior end. In a later paper (1897) he did place Symphyla in a division along with the classes Diplopoda and Pauropoda.

After a very careful study of the symphylans, and the literature pertaining to them, Schmidt (1895*a*) reached the conclusion that their position in nature should be between the Pauropoda and Diplopoda. Sinclair (1895) believed that they should be included among the Myriapoda and gave reasons for placing them there.

Silvestri (1901) found in *Projapyx* cerci with ducts and glands attached thereto, and stated that this was another character which served as a link between the Thysanura and Symphyla.

Hansen (1897) stated that not very far distant from the Thysanura was found *Scolopendrella* which formed a transition to the Chilopoda and Diplopoda. In 1903 he published his very complete work on Symphyla. He gave a good review of the literature, but confined his paper largely to classification. He described 24 species in the Symphyla, 12 *Scutigerella* and 12 *Scolopendrella,* all but 5 of which were new. He stated that what Latzel (1884*a*) thought to be *Scolopendrella notocantha* was the same as his species *Scolopendrella vulgaris. Scutigerella gratiae* and *Scolopendrella latipes* Scudder were listed as spurious or insufficiently described species. He also reëstablished *Scolopendrella microcolpa* Muhr.

Carpenter (1903), in his article on the relationship between the classes of Arthropoda, stated: "With confidence, therefore, we may postulate a scolopendrelloid ancestry for insects, centipedes and millipedes." In his conclusions he said: "The Insecta, Chilopoda, and Diplopoda may be derived from common symphylan ancestors, which branched off from the primitive Crustacea (proto-Leptostraca)." In 1905, in discussing the phylogeny of the arthropods, he used *Scolopendrella* as a sort of connecting link in binding the tracheate classes together, since it showed

affinities with the members of the several classes. In 1916 he set forth reasons why Symphyla, together with Diplopoda and Chilopoda, should be given class rank. Henning (1908) gave a historical review of the classification of Myriapoda which included the part played by Symphyla.

Bagnall, beginning about 1910, published a number of papers on Symphyla which dealt with classification and distribution (mostly British). He also named a number of new species and established the subfamily Scutigerellinae, which he said might later be raised to family rank by other workers.

Crampton (1918), in regard to phylogeny, stated:

> It is quite probable that ancestral "myriapods" were similar in many respects to the members of the "Symphyla-Pauropoda" group, and it would be a comparatively simple matter to derive these types from crustacean forms allied to *Bathynella* or other Anomostraca.

Tillyard (1931), on the other hand, did not believe in a crustacean ancestry, but in the development of his theory on the evolution of the class Insecta, he created a hypothetical ancestor for the various groups of myriapods and insects, and clearly brought out the relation of Symphyla to these groups.

Since 1910 a number of papers have appeared which deal with classification, and a few also which consider ecology and anatomy. During this period *Scutigerella immaculata* has risen to the rank of a serious economic pest, and since 1920 numerous important papers have been published on this subject.

Since most of the important articles published after 1910 are considered elsewhere in the text, no comments will be made here, with the exception of a few remarks on Verhoeff's outstanding work (1933–34). In this article he covered the entire field on Symphyla and gave an excellent review of much of the literature, although he overlooked several very important papers. Under his list of the more important works he completely left out all the publications dealing with the economic phases of the garden centipede, and, in general, all the recent American articles. Despite this, his work is probably the most valuable article published on Symphyla up to the present time.

Folsom and Wardle (1934) discussed Symphyla briefly, chiefly from the standpoint of classification and phylogeny. Imms (1934) also gave a short discussion from the same point of view. In 1936 Imms published a paper on the ancestry of insects in which he derived them from a symphylan ancestor. Calman (1936) also believed that the insects arose from a stock very similar to the present day symphylans.

SYSTEMATIC POSITION

SYNONYMY

Scolopendrella immaculata Newport (1845)
Scolopendrella americana Packard (1873)
Scutigerella immaculata (Newport) Ryder (1882)
Scutigerella californica Woodworth (1905*a*)

FULL CLASSIFICATION

For a long time there was some doubt as to the systematic position of the symphylans. Some of the early workers placed them with Chilopoda. While Newport (1845) included them with this class, he recognized that *Scutigerella immaculata* had distinctive characters and therefore erected the family Scolopendrellidae to include it. Ryder (1880) set up the order Symphyla, since his studies showed that they should be separated from the myriapods. Later, Symphyla was raised to class rank, and all present-day students of this group are in accord with this arrangement. While symphylans show some relationship to the insects, there is little doubt but that they should be included as a class among the myriapods. They are more closely related to the Pauropoda and the Diplopoda than to the Chilopoda, as many of the early investigators thought.

The full classification of the garden centipede is as follows:

Phylum	Arthropoda
Class	Symphyla Pocock (1893)
Order	Symphyla Ryder (1880)
Family	Scutigerellidae Ribaut (1931)
Subfamily	Scutigerellinae Bagnall (1913*b*)
Genus	*Scutigerella* Ryder (1882)
Species	*immaculata* Newport (1845)

The garden centipede has a very complex life history, and it is probable that this is true of other members of the class also. Consequently, great care should be exercised in naming new species. Different stages of the same organism may have been named as new species in the past. If possible, therefore, individuals should be kept alive and observations made to determine whether any changes take place. In this connection, Ribaut (1931) believed that the species *Scutigerella biscutata* described by Bagnall (1914*a*) was just a stage of the garden centipede, *Scutigerella immaculata*. Verhoeff (1933) likewise believed that this was a larva of *S. immaculata* in the stage in which there are 11 pairs of legs. If the posterior end of *S. biscutata* as compared with *S. immaculata* is correctly figured by Bagnall, and if the individual in question actually had 12 pairs of legs, it appears that he was dealing with a new species.

Hansen (1903*a*) noted numerous variations and stated:

In *Scutigerella,* at least, species show a special difficulty: specimens of the same species having acquired the full number of legs vary very much in size; this difference can be very large between specimens from the same locality or from different localities, and arises often, most probably, from the age of the individuals; but sometimes it is a real local variation, a remark already set forth by Latzel on *Scut. immaculata* in Austria. . . .

. . . The genus *Scutigerella* has caused me much trouble and I may advise future students not to establish new species without a very careful and prolonged examination of several forms, and never to establish a species on specimens not having acquired a full number of legs, or on specimens in which the legs of the twelfth pair are not quite as long and do not possess so many setae as those of the eleventh pair.

GENERA AND SPECIES OF SYMPHYLA

At the present time there are 54 known species of Symphyla throughout the world, and probably there are a great many more. A list of the genera and species follows:

Scolopendrella notacantha Gervais, 1839
S. anacantha Tömösvary, 1883
S. notella Hilton, 1933
S. numexta Hilton, 1933
Scolopendrellopsis microcolpa (Muhr, 1881) Bagnall 1913*b*
S. sensiferis Hilton, 1931
S. silvestrii (Hansen, 1903*a*) Bagnall, 1913*b*
S. pygmaea (Silvestri, 1902) Bagnall, 1913*b*
Symphylella isabella (Grassi, 1886) Silvestri, 1902
S. antennata (Hansen, 1903*a*) Bagnall, 1913*b*
S. brevipes (Hansen, 1903*a*) Bagnall, 1913*b*
S. cubae Hilton, 1931
S. delicatula (Bagnall, 1914*a*) Bagnall, 1913*b*
S. dunelmensis (Bagnall, 1914*a*)[5] Bagnall, 1913*b*
S. horrida (Bagnall, 1914*a*) Bagnall, 1913*b*
S. jacksoni (Bagnall, 1914*b*) Bagnall, 1913*b*
S. minutissima (Bagnall, 1914*a*) Bagnall, 1913*b*
S. neotropica (Hansen, 1903*a*) Bagnall, 1913*b*
S. pusilla (Hansen, 1903*a*) Bagnall, 1913*b*
S. santa Hilton, 1931
S. simplex (Hansen, 1903*a*) Bagnall, 1913*b*
S. texana (Hansen, 1903*a*) Bagnall, 1913*b*
S. vulgaris (Hansen, 1903*a*) Bagnall, 1913*b*
Scolopendrellina californica Hilton, 1931
Scutigerella immaculata (Newport, 1845) Ryder, 1882
S. armata Hansen, 1903*a*
S. biscutata Bagnall, 1914*a*
S. indecisa Attems, 1911

[5] In the paper cited as "Bagnall 1914*a*," published in 1914 but apparently read about 1911, Bagnall describes this as a variety of *isabella;* but later (1913*b*) he raised it to the rank of species.

S. spinipes Bagnall, 1914*a*
Neoscutigerella hanseni (Bagnall, 1914*a*) Bagnall, 1913*b*
Hanseniella Bagnall
subgenus: *Hanseniella unguiculata* (Hansen, 1903*a*) Bagnall, 1913*b*
H. angulosa (Hansen, 1903*a*) Bagnall, 1913*b*
H. caldaria (Hansen, 1903*a*) Bagnall, 1913*b*
H. californica Hilton, 1931
H. capensis (Hansen, 1903*a*) Bagnall, 1913*b*
H. chilensis (Hansen, 1903*a*) Bagnall, 1913*b*
H. dolosa Ribaut, 1914
H. neozelanica Chamberlin, 1920
H. nivea (Scopoli, 1763) Bagnall, 1913*b*
H. orientalis (Hansen, 1903*a*) Bagnall, 1913*b*
H. plebeia (Hansen, 1903*a*) Bagnall, 1913*b*
H. producta Ribaut, 1914
H. ruwenzorii (Silvestri, 1907) Bagnall, 1913*b*
H. subunguiculata (Imms, 1908) Bagnall, 1913*b*
H. tenella Ribaut, 1914
subgenus: *Scolopendrelloides crassicornis* (Hansen, 1903*a*) Bagnall, 1913*b*
S. pauperata (Hansen, 1903*a*) Bagnall, 1913*b*
Pseudoscutigerella americana Hilton, 1931
Tasmaniella hardyi Chamberlin, 1920
Geophilella pyrenaica Ribaut, 1913
Ribautiella zagnanadina Brölemann, 1926*b*
Symphylellina pachypoda Brölemann, 1931
S. californica Hilton, 1931
Symphylellopsis subnuda (Hansen, 1903*a*) Ribaut, 1931
S. arvernorum Ribaut, 1931

DISTRIBUTION

The wide geographical distribution of the garden centipede is roughly shown in figure 2. In Europe it is known to occur in a great many places. Its distribution there is well worked out, since it has been studied by a large number of workers in that area. On that continent it is known to extend rather far north. Schmidt (1895*a*) reported it as occurring at St. Petersburg (Leningrad) about 60° lat. N., and Ellingsen (1904) at Trondheim, Norway, about 63.25° lat. N. In both Norway and Sweden the garden centipede has been collected at about 60° lat. N. on several occasions.

In North America it is widespread, but its distribution is by no means completely worked out. It is known to occur in Canada in the Victoria district, in Mexico at Cordova, and in Cuba. In the United States it has been recorded in no fewer than thirteen states. Some of these are widely separated, which would indicate that further study will show the garden centipede fairly well distributed throughout the entire area. In this country it extends as far north as Salem, Massachusetts, about 42.30°

lat. N. (Packard, 1881); Lansing, Michigan, about 42.45° lat. N. (McDaniel[6]); Mt. Clemens, Michigan, about 42° lat. N. (Pettit, 1929); and Erie County, New York, about 42.5° lat. N. (Taylor, 1928). The most northerly point in North America at which it has been found is Victoria, British Columbia, 48.27° lat. N.

Buenos Aires appears to be the only place in South America where the garden centipede is definitely known to occur. Silvestri (1899) re-

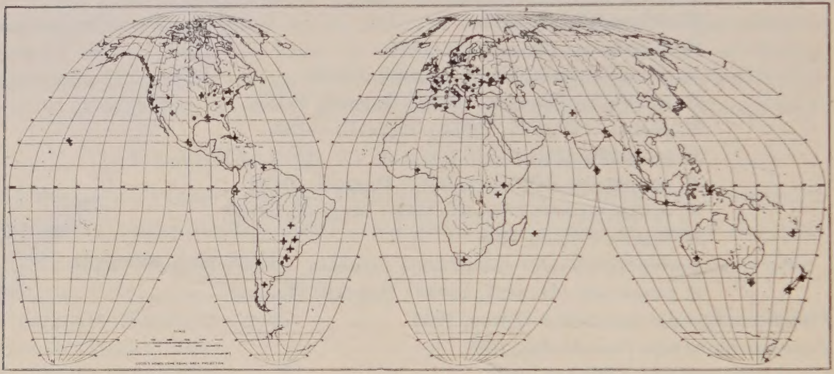

Fig. 2.—Geographical distribution of Symphyla throughout the world. Dots represent the garden centipede, *Scutigerella immaculata* (Newp.), and crosses represent all other Symphyla. (Goode Base Map No. 101HC has been used with the permission of the University of Chicago Press, copyright owners.)

ported it from Chile, but Hansen (1903*a*) showed that what Silvestri thought to be the garden centipede, *Scutigerella immaculata,* was a new species, *Scutigerella chilensis.* Later Silvestri made this correction.

To the present time the garden centipede does not appear to be widespread in Africa. In the northern part it has been reported from several localities in Algeria and Tunisia.

The present writer knows of no definite records of it from Asia or Australia. Pocock (1894) reported it from Java and Sumatra, but Hansen (1903*a*) stated that he was dealing with a new form, *Scutigerella orientalis.*

Not only does the garden centipede occur rather far north, but it has also been collected at high elevations. Friedel (1928), working in Austria, reported finding it in the Alps at 3,000 meters (9,842 feet) and Faes (1902) found it at 2,000 meters (6,561 feet).

In Europe it extends further north than in North America. Its northern limits of distribution seem to be restricted by low winter temperatures. After studying weather records, conditions appear unfavorable for the survival of the garden centipede where the expected minimum

[6] McDaniel, E. I. In letter to author, October 30, 1933.

TABLE 1

SOME IMPORTANT CLIMATIC CONDITIONS IN REGIONS OF THE WORLD WHERE THE GARDEN CENTIPEDE OCCURS

Station	Latitude, degrees north	Elevation, feet	Temperature, °F					Rainfall				
			Mean annual temperature	Mean warmest month	Mean coldest month	Mean of maximums observed each year	Mean of absolute minimums observed each year	Total amount, inches	Mean maximum		Mean minimum	
									Amount, inches	Month	Amount, inches	Month
Trondheim,* Norway	63.25	131	40.46	57.20	27.32	81.86	− 0.04	31.10	3.42	Jan.	1.49	May
Oslo,* Norway	59.55	82	42.44	63.14	24.44	87.44	− 2.20	25.39	3.54	Aug.	1.46	Feb. and March
Stockholm,* Sweden	59.16	144	42.26	62.24	26 42	83.48	− 1.48	21.57	2.91	Aug.	1.30	Feb. and March
Leningrad,† U. S. S. R.	59.55	32	38.66	63.86	15.26	84.20	−20.20	18.90	2.75	Aug.	0 78	Feb.
Copenhagen,* Denmark	55.40	16	45.86	62.60	31.28	84.20	8.60	22.60	2.72	Aug.	1.34	Jan. and Feb.
Buffalo,† U. S.	45.55	787	47.12	70.16	24 00	89.60	− 7.60	38.19	3.54	Oct.	2.36	March
Chicago,† U. S.	41.50	820	48.56	72.32	23.72	95.00	−14.80	34.65	3.94	June	1.97	Jan.
Boston,† U. S.	42.20	131	48.74	71.24	26.96	95.00	− 5.80	44.87	4.33	Aug. and Nov.	3.15	Jan.
Salt Lake,† U. S.	40.44	4,396	51.80	76.28	28.94	98.60	− 2.20	16.14	2.36	April	0.04	July
Pilatus,‡ Switzerland	47.00	6,784	32.54	46.58	20.84	68.00	− 6.34	55.92	7.16	June	1.30	Dec.
Santis,‡ Switzerland	47.15	8,202	27.32	41.00	16.16	59.90	− 9.40	95.74	11.93	July	4.80	Nov.
Sonnblick,‡ Austria	47.80	10,190	20.30	34.34	7.52	49.82	−23.08	69.29	6.69	Oct.	4.13	Sept.
Innsbruck,‡ Austria	47.47	1,968	46.22	64.04	26.06	88.34	1.40	33.58	5.00	July	1.54	Jan.
Paris,‡ France	48.52	164	51.26	64.58	37.40	92.84	11.66	23.74	3.11	Dec.	1.10	Feb.
London,† England	51 30	131	49.64	63.14	38.12	87.80	17.60	24.40	2.76	Oct.	1.57	April
Agram,‡ Yugoslavia	45.48	534	52 16	70.88	31.82	92.12	8.24	35.43	3.94	June	1.81	Jan.
Coimbra,‡ Portugal	40 10	459	59.36	70.88	48.56	100 76	30.92	35.20	4.37	Nov.	0.59	Aug.
Rome,† Italy	41 54	164	59 72	76.64	44.06	95.00	26.60	31.50	4.72	Oct.	0.79	July
Catania,† Sicily	37.30	98	64.94	79.52	51.44	98.60	35.60	20.87	3.54	Nov.	0.00	July
Tunis,† Tunisia	36 40	131	64.22	79.88	49.64	109.40	33.80	18.11	2.36	March and Dec.	0.39	July
Los Angeles,† U. S.	34 30	360	60 26	68.54	53.06	100.40	33.80	17.32	3.94	Dec.	0.00	Aug.
San Francisco,† U. S.	37.45	196	54 86	59.36	49.46	89.60	33.80	23.62	5.12	Dec.	0.00	Aug.
Sacramento,† U. S.	38.37	131	59.54	72.32	45.68	104.00	28.40	20.86	4.33	Dec.	0.00	July
Bakersfield,§ U. S.	35.22	492	63.70	81.40	47.20	111.60¶	22.00¶	5.62	1.04	Jan.	0.02	July
San Antonio,† U. S.	29.25	787	67.82	82.40	51.08	100.40	19.40	29.92	3.94	Aug.	1.57	Oct. and Jan.
Havana,† Cuba	23.80	65	76.64	81.86	70.34	96.80	53.60	51.57	7.48	Oct.	1.97	March
Mexico City,† Mexico	19 30	7,480	59.90	64.94	53.42	86.00	33.80	23.23	4.72	Aug.	0.00	Jan.
Honolulu,† Hawaii	21.18	65	73.94	77.54	70.16	86.00	55.40	35.43	5.12	Nov.	1.97	Jan.
Buenos Aires,† Argentina	34.40‖	65	61.88	73.58	50.18	93.20	32.00	36.61	4.72	March	1.97	July

* Data in: Birkeland, B. J., and N. J. Föyn. Klima von Nordwesteuropa und den Inseln von Island bis Franz-Josef-Land. Handbuch der Klimatologie [Berlin] **3** (L): 134. 1932.

† Data in: Koppen, W. Grundriss der Klimakunde. 388 p. Walter De Gruyter und Co., Berlin and Leipzig. 1931.

‡ Data in: Alt, E. Klimakunde von Mittel- und Südeuropa. Handbuch der Klimatologie [Berlin] **3** (M): 288. 1932.

§ Data in: United States Department of Agriculture. Weather Bureau, Climatological data. California section.

¶ Mean for 1922 to 1933, inclusive.

‖ Latitude, degrees south.

temperature drops to about —29°C (—20°F). This same thing appears to hold true for its distribution as far as elevation is concerned, since lowest expected temperatures in the Alps for places at 2,000 to 3,000 meters range from about —21°C (—6°F) to —30°C (—23°F).

Nothing can be said of the southern limits to which the garden centipede may be found, but it probably extends rather far into the tropics, since the climate of the Hawaiian Islands seems to be so well suited to its development.

Fig. 3.—Distribution of the garden centipede in California, by counties.

In California the garden centipede has been found in Bakersfield, which has a hot dry climate. It is also found in places where the climate is wet and humid. Judging from the above discussion, this organism can evidently occur over a wide climatic range. This is undoubtedly possible because it inhabits the soil and can penetrate to a depth of 3 feet or more, which is unquestionably an important factor in its adaptation to the varied climatic conditions under which it occurs. Table 1 has been prepared to show some of these climatic variations, and includes data from stations over the world where the garden centipede is known to occur. Data on latitude, elevation, temperature, and rainfall are included. The information given in table 1 probably comes close to defining the climatic area in which it can exist, with the exception of the tropical region where conditions are undoubtedly favorable for its development.

It is widespread in California, occurring in at least 24 of the 58 counties. In a brief survey made during the summer of 1934 it was found with ease in areas not previously reported. In fact, this one study would lead one to believe that the garden centipede is probably present in every county of the state. In this survey it was found at least once in every three examinations made. Up to the present time it has not been found outside the lowlands, but as soon as possible an investigation will be made to determine to what extent it occurs in the mountains of the state. Figure 3 indicates the counties in which it is known to occur at this time.

Figure 2 also gives the distribution of Symphyla other than the garden centipede, *Scutigerella immaculata* (Newp.). No attempt has been made to show the distribution of the individual species. A cross merely indicates the presence of one or more species of Symphyla. The map

shows that some members are well distributed in the tropics. In fact, with the exception of the colder regions, the various species are found widely scattered over most of the world. The present writer has no record of Symphyla from China and Siberia, although they probably occur in these areas.

The distribution of the garden centipede by countries is given in the following tabulations:

Africa
- *Algeria:* Hansen (1903*a*, 1903*b*), Bagnall (1915)
- *Tunisia:* Silvestri (1896)

Europe
- *Austria:* Latzel (1884*a*), Hansen (1903*a*), Friedel (1928), Verhoeff (1933–34)
- *Corsica:* Léger and Duboscq (1903)
- *Crete:* Attems (1902)
- *Czechoslovakia:* Rosicky (1876), Muhr (1881), Packard (1881), Latzel (1884*b*), Verhoeff (1933–34)
- *Danzig Free State:* Menge (1851)
- *Denmark:* Hansen (1903*a*)
- *England and Scotland:* Newport (1845), Hansen (1903*a*), Evans (1909, 1919), Bagnall (1911, 1912, 1913*a*, 1914*a*, 1914*b*, 1917), Theobald (1912), Brade-Birks (1920), Walton (1930), Staniland (1932), Kearns and Walton (1932), Verhoeff, (1933–34)
- *France:* Gadeau de Kerville (1883), Moniez (1893), Hansen (1903*a*), Brölemann (1910, 1926*a*), Feytaud (1925, 1926), Verhoeff (1933–34)
- *Germany:* Muhr (1881), Hansen (1903*a*), Ellingsen (1906), Verhoeff (1933–34)
- *Hungary:* Daday (1889*b*), Latzel (1884*a*), Verhoeff (1933–34)
- *Ireland:* Carpenter (1895), Selbie (1912), Bagnall (1914*a*), Foster (1915*a*, 1915*b*, 1919)
- *Italy and Sicily:* Grassi (1886), Silvestri (1894), Hansen (1903*a*, 1903*b*), Verhoeff (1933–34)
- *Norway:* Porat (1887), Ellingsen (1904), Attems (1903)
- *Poland:* Karlinski (1883*a*, 1883*b*)
- *Portugal:* Almeida (1930)
- *Romania:* Daday (1889*a*)
- *Russia:* Schmidt (1895*a*), Latzel (1884*a*), Lignau (1903, 1905), Attems (1903), Verhoeff (1933–34)
- *Spain:* Balearic Islands (Brölemann, 1910)
- *Sweden:* Porat (1889), Ellingsen (1903), Hansen (1903*a*), Attems (1903), Verhoeff (1933–34)
- *Switzerland:* Rothenbühler (1899), Faes (1902), Holzapfel (1932)
- *Yugoslavia:* Attems (1929)

North America
- *Canada:* Victoria district of British Columbia (Hyslop, 1927)
- *Cuba:* Twenty miles south of Havana (Hilton, 1931)
- *Mexico:* Cordova (Packard, 1886); Mexico Valley (Hilton, 1931)
- *United States:*
  - California: Widely distributed

Colorado: Numerous locations (List[7])
Georgia: Billy's Island, Okefenokee Swamp (Chamberlin, 1918)
Illinois: Widely distributed (Forbes, 1883; Davis, 1912; Compton, 1930; Illinois, 1929, 1930; Flint, 1932)
Indiana: Widely distributed (Davis, 1924, 1928, 1931; Riley, 1928, 1929; Sheaffer, 1930)
Kentucky: Mammoth Cave (Packard, 1881)
Massachusetts: Salem (Packard, 1881)
Michigan: Probably generally distributed over part of the state (McDaniel, 1931; Pettit, 1929)
New Jersey: North Plainfield (Headlee[8])
New York: Nyack (Herrick, 1927); Erie County (Taylor, 1928)
North Carolina: Jacot (1936)
Ohio: Widely distributed (Williams, 1907*a*, 1907*b*; Gossard, 1925; Filinger, 1928, 1931*a*; Parks, 1930; Mendenhall, 1931; Hauser, 1932)
Oregon: Numerous localities. Symphylans [probably *Scutigerella immaculata* (Newp.)] (Lovett, 1921; Oregon, 1926, 1928, 1930)
Pennsylvania: Philadelphia Park (Ryder, 1880; Thomas, 1928); Bustleton and Kennett Square (Thomas, 1929); southeastern Pennsylvania (Thomas, 1930)
Texas: Austin (Hansen, 1903*a*)
Utah: Symphylans [probably *Scutigerella immaculata* (Newp.)] Numerous locations (Knowlton, 1932)
Virginia: Widespread, probably throughout all the South (Bailey[9])
Washington, D. C.: Smith (1933)

South America
Argentina: Buenos Aires (Hansen, 1903*a*); Patagonia (Attems, 1903)

Islands not already mentioned
Azores: Silvestri (1896), Attems (1903)
Hawaii: Widespread in pineapple growing areas (Illingworth, 1927*a*, 1927*b*, 1928*a*, 1928*b*, 1929*a*, 1929*b*; Godfrey and Illingworth, 1928). Illingworth (1927*a* and 1927*b*) speaks of symphylan only, but organism probably *Scutigerella immaculata* (Newp.).

EXPERIMENTAL METHODS

STORAGE CULTURES

As thousands of garden centipedes were used in carrying out this investigation, it would have been difficult to gather these in the field as needed. In order to secure an ample and continuous supply, a special type of storage culture was developed. An intact section of a silty clay subsoil, permeated with countless fine cavities, was placed in a battery jar and covered with a pane of glass. The soil used was always obtained from fields heavily infested with the animal. The jars were stocked with additional garden centipedes obtained from field collections. A lettuce leaf was placed over the surface of the soil in the jar and was replaced from

[7] List, George M. In letter to author, November 13, 1933.
[8] Headlee, Thomas J. In letter to author, November 8, 1933.
[9] Bailey, J. W. In letter to author, November 26, 1936.

time to time as needed. In such a culture they increased rather rapidly, and four to six jars furnished more than enough material.

Specimens were obtained from the culture by lifting out the lettuce leaf and jarring it over a glass container. This freed the garden centipedes from the leaf and those of the desired stage could be collected with a camel's hair brush. This was possible because in such cultures the garden centipedes come to the surface and feed readily on the lettuce. Although they could also be collected from the surface of the soil at the time the lettuce was removed, in most of the experimental work conducted, only those obtained from the leaf were used. This was done to obtain, as nearly as possible, individuals in the feeding phase.

Other organisms also became established in these cultures, notably springtails, which were sometimes present by the hundreds. These did not appear to interfere in any way with the garden centipedes.

REARING DISHES

The storage cultures, while suited for general observations, are not satisfactory for exact experimental studies. A culture suited for this type of work was developed by Filinger (1928, 1931*a*), which is a modification of the method used by Searls (1928) for the rearing of the cucumber beetle. These rearing dishes are made by pouring "muck plates" into stender dishes (10 parts plaster of Paris mixed with 3 parts finely ground muck). Such plates are kept moist, and the garden centipedes live on the surface. Lettuce has been found to be a very satisfactory food.

The rearing cultures used in this investigation were prepared somewhat differently from those of Filinger. A silty sediment was used instead of muck, and animal charcoal was added to the mixture, which gave the plates a very dark color. This dark background greatly facilitated locating molted skins, and was particularly useful when studying the young and searching for the early-stage molts. A mixture which was frequently used contained 10 parts plaster of Paris, 3 parts soil, and 1 part charcoal. The materials were thoroughly mixed by shaking, and enough water was added so that after violent stirring the material had the consistency of thick cream. This was then poured into stender dishes to about the depth of ¼ inch and allowed to set. When experiments were of long duration and it was necessary to add moisture from time to time, distilled water was used. The same garden centipedes have remained alive for nearly four years in the same culture, which shows that these dishes maintain favorable conditions for their livelihood. The two sizes of dishes most frequently used were 60 mm or 50 mm in diameter by 30 mm deep.

ETHERIZING

In the course of this investigation it was found necessary to make numerous examinations of the garden centipedes, and often the same individuals were closely observed at varying intervals. This required complete inactivity of the specimens studied. In such cases etherizing them gave the best results. Ether, unless used with care, may be injurious to the garden centipede; serious injury is certain to occur if the liquid ether comes in direct contact with them.

Two methods of etherizing were used: One was to take a piece of cotton moistened with ether U.S.P. and hold it with a pair of forceps in the culture containing the garden centipede. Although the forceps will not permit the lid to close down tightly, this is not necessary since the garden centipedes are very susceptible to the gas. In fact, if a natural position is desired, rapid etherization should be avoided because it has the tendency to make them curl. Anesthetizing for a period long enough to enable one to count the antennal segments, and make a few other general observations (usually 2 to 5 minutes), apparently has little deleterious effect upon the organisms. The second method was to place a small cotton plug moistened with ether against the inside of the container. When the garden centipedes had enough ether to become quiet, the plug was removed. Later, if necessary, it was replaced. The lid need not be placed on the container since enough ether is given off from the cotton to keep the garden centipedes inactive. In making lengthly examinations this was the method most frequently used.

When the second method is used, the garden centipede should never be left in the examining container, for enough ether is usually absorbed by the substratum to be lethal to the organism when the cover is replaced on the culture. Toward the end of the investigation a single experiment was designed to test whether repeated etherization had any effect whatever upon the garden centipede. A few of the etherized individuals appeared to be somewhat stunted. But since both the etherized and check groups contained only a small number of individuals, the results were not very conclusive, and further work on the effects of ether is desirable. However, many garden centipedes were etherized a number of times without any apparent ill effects.

MICROSCOPIC EXAMINATION

Binocular microscopes were used in examining living material. Unless properly illuminated, the finer structures of the garden centipede are very difficult or impossible to determine. An ordinary desk lamp was not suited for detail studies. A satisfactory type of light was given by a

Spencer high-power Mazda microscope lamp (500-watt globe) equipped with diaphragm so that the amount of light could be regulated.

A microscope was always used in examining mounted material. Two types of mounting media were used: Berlese's medium, and the same modified according to the method of Lamiman[10] in which iodine is added. The latter gave the best results.

When possible, all drawings were made from living material; where mounted specimens were used, the fact is noted.

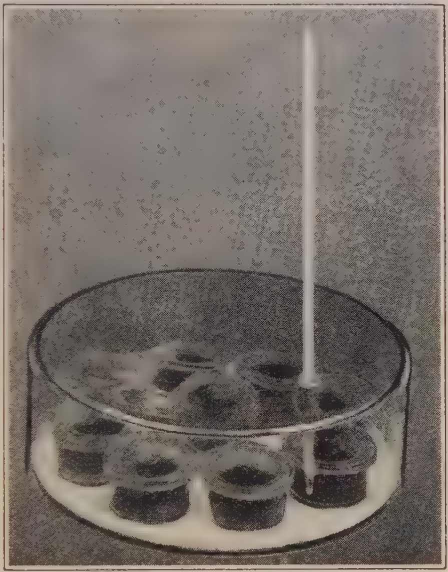

Fig. 4.—Unit used for insuring a uniform temperature in the constant-temperature cabinets.

TEMPERATURES

Since the garden centipede lives for several years, much of the laboratory work was carried on at room temperature, because it would have been difficult to keep constant-temperature cabinets going over a period of years. This was done in a room having a north exposure, in which thermographic records showed the temperature to be rather constant throughout the year, averaging very close to 21° C.

Considerable work was done in constant-temperature cabinets. During the last two years of the investigation, cabinets were available that did not fluctuate more than ± ½° C. In order to insure uniform conditions for any experiment, the individual cultures involved were placed in large moisture dishes. A pad of moist cotton was placed in the bottom of the dish and a hole was bored in the cover through which a thermometer was inserted. The temperature recorded by the thermometer was assumed to be the same as that prevailing in the individual cultures. This apparatus is shown in figure 4. In the cabinets the cultures were always shielded from the direct source of heat.

[10] Data obtained from unpublished material by J. Lamiman, Division of Entomology and Parasitology, University of California.

TROPISM AND BEHAVIOR

The storage cultures were valuable in that they afforded an opportunity to observe some habits of the garden centipedes under laboratory conditions. They are negatively phototropic, but this response is not very strongly developed for they appear to come to the surface and feed without any hesitation. They also come to the outside of the soil section at any point, and from all appearances do not react very strongly to light. It is not uncommon to find them lying perfectly motionless on the surface of the soil where they are fully exposed. When they are in this condition, tapping on the side of the container apparently has little effect upon them.

When in motion the garden centipedes keep their antennae constantly moving, while when feeding they are as a rule held backwards. If disturbed, they move very quickly and retreat into the soil as rapidly as possible. If their antennae are barely touched with a camel's hair brush or other instrument, they reverse their course with lightning speed. Like observations were made by Menge (1851), while Verhoeff (1933–34) stated that in turning around, the posterior end stays in place acting as a pivot.

The conditions in the cultures seem to be favorable for the garden centipedes, which multiply rapidly, and in every culture so far started, they have maintained themselves. The very young never come to the surface of the soil and apparently do not come out to feed until they have molted for the second time. Of the great number of feeding individuals examined, none have been observed with fewer than 8 pairs of legs. Indications are that they come out to feed shortly after they reach this stage. Up to this stage they are apparently more or less gregarious. This is further indicated by the fact that often in looking over soil the molted skins of the very young stages are found clustered together.

LIFE HISTORY

The garden centipede has a rather complicated life history. Early investigators had no clear conception of the immature stages, and, in some cases, were in doubt concerning the systematic position of the adults. Gervais (1847) thought that the first specimens of *Scolopendrella notocantha* which he collected were young *Geophilus* and called them *Geophilus* junior."[11] Fabre (1855) thought that they were young *Cryptops*. Latzel (1884*a*) believed that the young probably had 3 pairs of legs at

[11] Gervais (1847) stated that this descriptive name was used in a previous publication (Ann. Soc. Entom. de France, 1st series, 1836), but the present writer has been unable to locate this article.

the time of hatching, as did Davis (1912) and Attems as late as 1926. Latzel also thought that a gradual postembryonic development took place from time to time until sexual maturity, in which segments with legs were added between the end segment and the last segment which carried legs. Although he observed larvae with 6, 7, 8, 9, 10, and 11 pairs of legs, he did not realize that those with 6 pairs were newly hatched. Attems (1926) and Williams (1906) also observed specimens with 6 pairs, but later Williams (1907*a*, 1907*b*) stated that the larvae hatched with 7 pairs of legs. Feytaud (1926) and Illingworth (1928*a*) also made this error. If the specimens observed by Williams were the garden centipede, *Scutigerella immaculata*, it is likely that he was examining larvae after the first molt; but they should have had 12 antennal segments instead of 6 as he reported. Since the newly hatched garden centipedes molt a day or two after hatching, it is possible that some of his observations were made after the first molt. Newport (1845) reported finding specimens with 9, 10, and 11 pairs of legs, while Menge (1851) stated that he found only one with 11 pairs.

Wymore (1924*a*, 1924*b*) gave a fairly good description of the newly hatched young; later (1931) he gave an account of the very immature stages, but did not discuss the later stages in detail. Filinger (1928, 1931*a*) gave one of the best accounts of the early stages, although his descriptions were lacking in completeness. Ribaut (1931) has published the most excellent and comprehensive discussion of the larval stages to date, while Verhoeff (1933–34) reviewed the literature which deals with the immature stages.

IMMATURE STAGES

Egg.—The eggs of the garden centipede are pearly white when first laid and are covered with a network of tiny ridges which serve to distinguish them from those of other organisms (figs. 5 and 7, *A*). As the incubation period is extended they become darker, until just before hatching they assume a light-tan color. The eggs are laid in runways in the soil, a single cluster containing sometimes as many as 25, although the usual number is 9 to 12. In the spring the present writer has gathered the eggs within a few inches of the soil surface, but as the soil dries, the garden centipedes tend to deposit them deeper.

A careful study of the incubation period has been neglected. In a field laboratory, during the winter and early spring of 1931, eggs hatched in 26 to 28 days. In the laboratory at Berkeley the incubation period ranged from 11 to 23 days. Other investigators in general report a shorter period than here noted. Filinger (1928) stated that the eggs hatched in about 14 days at room temperature; later (1931*a*) he gave the

incubation period as 10.8 days at about 70° F; Riley (1929) gave the time as a week to 10 days; Sheaffer (1930) as about 10 days; and Wymore (1931) as within 10 days during the early summer; while Compton (1930) noted it to be 8 to 21 days.

Considerable difficulty was encountered in this investigation in getting the eggs to hatch. In many cases they were attacked by molds soon after they were laid. Some investigators have reported that this occurs if the female is not present to free them from the fungus growth. This is apparently not correct because many eggs have been hatched in cultures free from all individuals, while in other cases, groups of eggs have been covered with mold in the presence of the garden centipedes. Since moisture seems to be one of the important factors favoring the growth of mold, the rearing dishes should be kept rather dry when trying to hatch eggs. Even then there is no assurance that the eggs will not mold. In the same culture one group of eggs will be attacked while the next one laid will hatch perfectly. In all cases observed it was noted that the eggs of a given cluster all hatched within a short time of one another.

Fig. 5.—Eggs and newly hatched first-instar larvae. A second-instar larva to the extreme upper right. (× 8.)

Since a large number of individuals were used in these experiments, an opportunity was afforded to study the stage of development at which egg laying begins. When the garden centipedes were held at 28° C, it was found that some began to lay between the seventh and the eighth molts. From those held at room temperature (about 21° C) the first eggs were obtained between the ninth and tenth molts. After this period, eggs were laid from time to time and have been obtained from group cultures after more than two and one-half years. A little less than three months was the shortest period which elapsed between hatching and the beginning of egg laying, but in general, the time necessary exceeded this considerably. Filinger (1931*a*) reported the time required for garden centipedes to reach sexual maturity at room temperature as 40 to 60 days. These figures probably represent the time elapsed until they passed through the sixth molt and do not refer to egg laying.

Some interesting observations were made in regard to egg deposition between molts. In all cases egg laying took place after the halfway period and usually a very short time before the garden centipedes passed into the next molt. The shorter the period between molts, the nearer the half-way-mark egg deposition occurred. Table 2 has been prepared in order to convey a clearer picture of these time relations.

First Instar.—When first hatched the young differ greatly from the adults. They are not very active, are sparsely clothed with rather long

TABLE 2

RELATION OF EGG LAYING TO MOLTING*

Total days between molts	Days from last molt to egg laying	Days to next molt	Total days between molts	Days from last molt to egg laying	Days to next molt
23	13	10	51	45	6
24	17	7	56	48	8
25	14	11	60	56	4
26	20	6	60	52	8
27	19	8	63	55	8
28	19	9	63	57	6
30	18	12	65	56	9
32	24	8	68	54	14
36	24	12	14†	10	4
38	32	6	17†	11	6
42	33	9	26†	23	3
44	34	10	29†	17	12
46	37	9	31†	22	9
48	43	5	31†	28	3

* Note that egg deposition occurs just a short time before molting.

† 28° C constant-temperature chamber.

hairs, have 6 pairs of legs, and 6 obvious antennal segments. The second antennal segment is peculiarly formed. It is greatly elongated and the apical fourth looks very much like the other segments, whereas the basal three-fourths appears as a cylindrical unsegmented membrane enclosing 4 more or less fully developed segments, and there are other segments that extend into the base of the first segment as shown in figure 6, *B*. If the membrane is ruptured, these segments become quite normal in appearance (fig. 6, *C*). They are only clearly visible in the cleared, mounted specimens, although they are indicated by rings in the living forms.

The posterior end of the body is much enlarged and its general structure is very different from that of any other stage. The enlargement is due mainly to the numerous unexposed parts which it contains; some of these are fully formed while others are not more than buds. The seventh pair of legs is well developed but is nearly completely enclosed in a membrane which hold them close to the body. If they are freed from

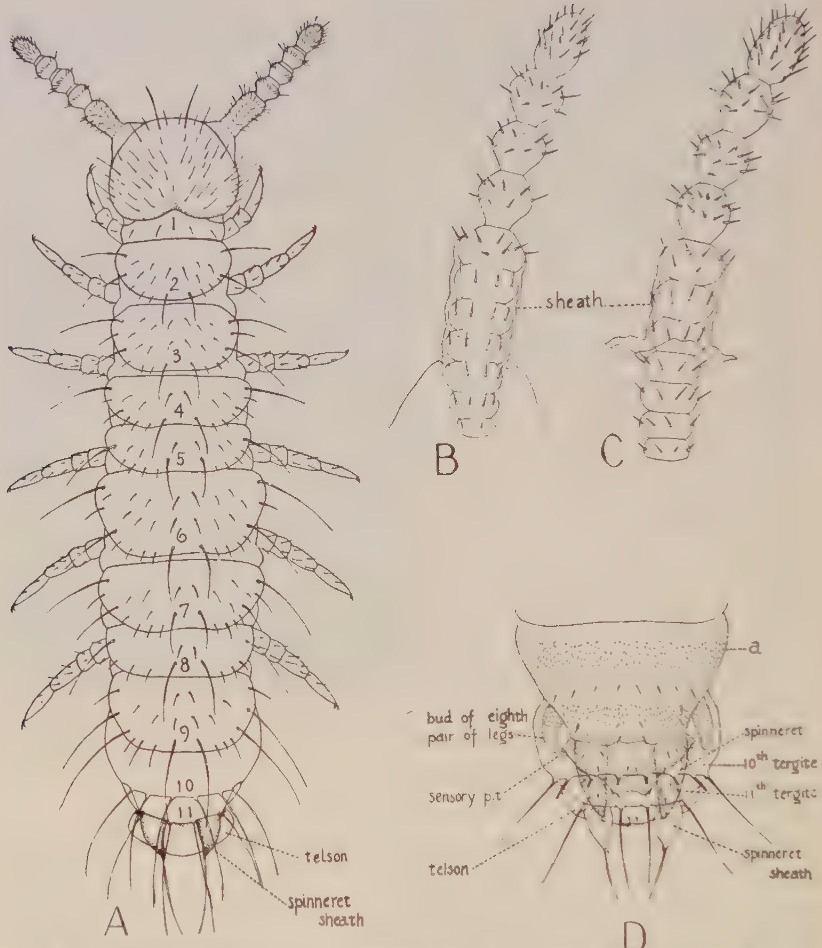

Fig. 6.—First-instar larva of garden centipede: *A*, Dorsal view (× 90). Note the elongated second antennal segment and the enlarged caudal end. Within this area are the numerous structures referred to in the text. The bulge on either side is probably due to the ensheathed seventh pair of legs. *B*, Antenna (× 180) as seen in a cleared, mounted specimen. Note the very elongated segment, which is made up of numerous segments enclosed in a sheath; *C*, same, with membrane ruptured and the basal portion partly broken away. *D*, Posterior region (× 110) as seen in a prepared mount where enough pressure has been applied to the cover glass to free the seventh pair of legs, and to force the integument posteriorly and reveal the enclosed structures; *a*, tergite which shows up as the last and tenth scutum in the second-instar larva.

this membrane, they become quite normal in appearance. Posterior to the seventh pair of legs, a pair of buds can be seen which, judging from their position, must be the beginning of the eighth pair of legs.

There are two structures present at the posterior end which have the appearance of small spinnerets, but mounted specimens show that these

probably only enclose the true spinnerets and may be called spinneret sheaths. In cleared specimens the developing spinnerets can be plainly seen through the integument. Their general shape and size is that of the functional spinnerets. They arise at the posterior margin of the tenth tergite and extend backward so that their apical ends project into the spinneret sheaths. These organs are covered with short hairs and a scattering of spines, similar to the spinnerets in the next stage.

The sensory organs also seem to be fairly well developed within the caudal end of the body. They show up rather plainly, although they seem to lack the long sensory setae which are so well developed in later stages. All the internal structures above described can be most distinctly seen if enough pressure has been applied to the cover glass, so that the seventh pair of legs is freed from its enclosing membrane.

Figure 6 *D* shows a drawing of the posterior end of a first-instar larva treated as described above. The pressure on the cover slip has forced the integument posteriorly revealing the enclosed structures. This integumental covering probably has mainly a protective function. It is not surprising that the structures which it covers are well developed, since molting, or ecdysis, occurs 24 to 48 hours after hatching.

There appear to be 11 dorsal plates, or scuta, but this seems unlikely since there are only 10 in the following stage. The first 9 are rather similar to those found in the older forms. There is some doubt as to the determination of the last 2 scuta. At the posterior margin of each of these there is a row of long hairs which arise from small protuberances. This character sets them off from any of the others. Possibly instead of 2 scuta there is in reality only 1, although 2 tergites are clearly defined. This might be considered as a single scutum composed of an anterior and posterior tergite, in which case the total number of scuta would be 10 and not 11. An enlarged drawing of a larva in this stage is shown in figure 6 *A*.

Second Instar.—Within 48 hours after hatching at room temperature the garden centipedes molt, after which their general appearance and habits become much the same as those of the adults, although their heads are rounder than in the mature form. Their activity is still somewhat like that of the first instar. The number of antennal segments is increased to 13, and a pair of legs is added. There are only 10 dorsal scuta, which means a reduction of one if the first instar larvae are considered to have 11. The spinnerets make their appearance as functional organs, and the posterior sensory setae come into prominence. Figure 7, *C* shows a larva in this stage of development.

Third Instar.—After the next molt another pair of legs is added, and

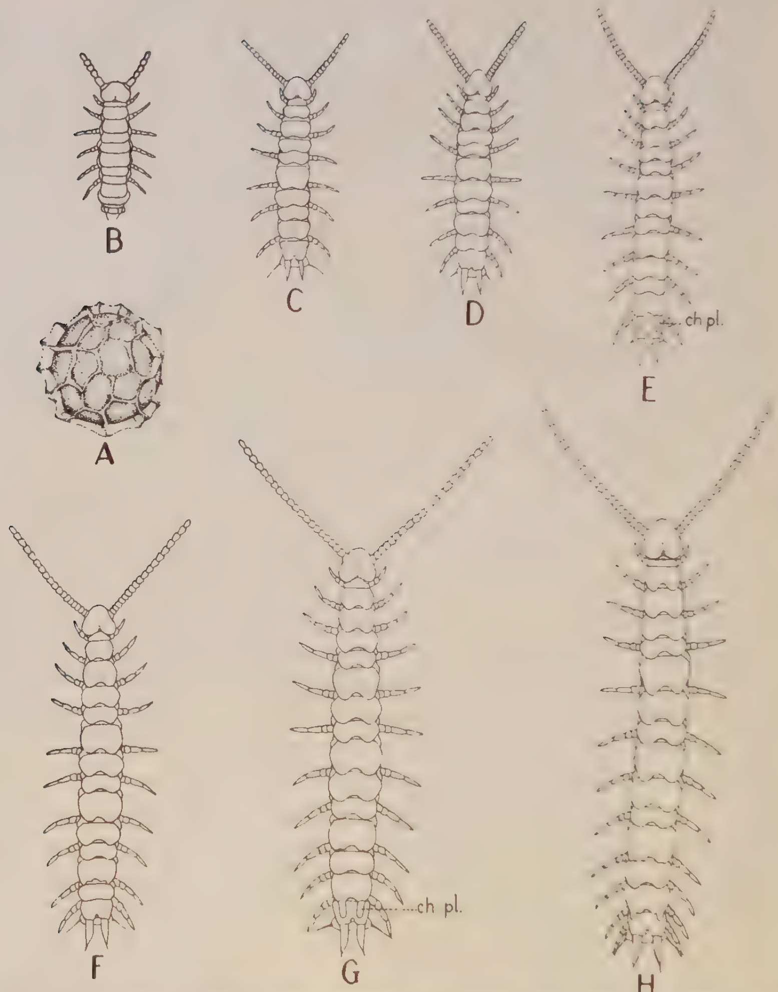

Fig. 7.—Successive stages of development of the garden centipede: *A*, egg (× 40); *B*, first instar; *C*, second instar; *D*, third instar; *E*, fourth instar; *F*, fifth instar; *G*, sixth instar; and *H*, seventh instar. *Ch. pl.* Chitinous plate. (*B-H*, × 17, same magnification as adult in fig. 10.)

the antennae have 15 segments. The number of dorsal scuta is increased to 11 (fig. 7, *D*).

Fourth Instar.—After the third molt (fig. 7, *E*) the individual usually has 17 antennal segments. Another pair of legs is added, and the dorsal scuta are increased by 2, making the total number 13. The new scuta are apparently added just in front of the last segment. A chitinous plate, which extends over a good portion of the last segment, is attached to each posterior lobe of the next to the last scutum (fig. 7, *ch. pl.*).

Fifth Instar.—With the fourth molt (fig. 7, *F*) the number of antennal segments is usually increased to 19, although the number added varies. The tenth pair of legs is added as well as another scutum. Here we find proof that the new scutum is added just in front of the last segment, for the scutum which supported the chitinous projections in the previous molt is now third from the end. The chitinous plates have been lost, but the posterior margin has a more or less scalloped appearance, which is somewhat variable in different individuals. Ribaut (1931), in his study of the immature stages, noted structures which he calls "cones pygidial." These are found laterally near the posterior end of those larvae of the third and fifth instars having 8 and 10 pairs of legs, respectively (fig. 8, *A* and *B*). According to Ribaut they occur where new tergal formations are not important and are reabsorbed when the dorsal part is greatly developed.

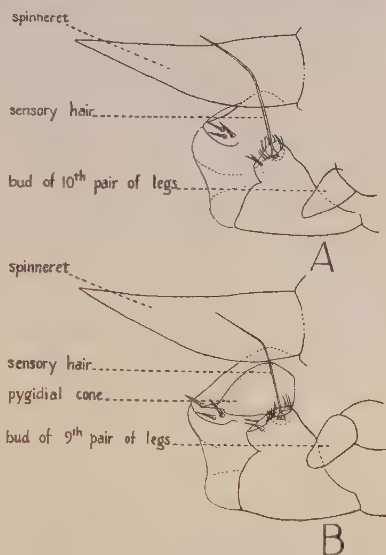

Fig. 8.—*A*, Posterior region of the garden-centipede larva with 9 pairs of legs; *B*, same of larva (earlier instar) with 8 pairs of legs as seen from the side. Note the absence of the pygidial cone in *A*. Drawn from mounted material. (× 170.)

Sixth Instar.—With the fifth molt (fig. 7, *G*) usually 2 or 3 more segments are added to the antennae. Another pair of legs and a scutum also make their appearance. As in the third molt, the new scutum contains the chitinous projections. The organism now has 15 dorsal scuta, the number found in mature individuals. The scutum which showed the scalloped effect in the preceding molt still retains this character but to a lesser degree. Its position is now fourth from the posterior end and twelfth from the anterior end. This relation to the anterior end has remained constant since its addition.

Seventh Instar.—The sixth molt (fig. 7, *H*) usually adds 2 to 4 more antennal segments. Another pair of legs appears, making a total of 12, the number found in mature specimens. The twelfth scutum may still show a slightly scalloped effect, while the fourteenth, which is next to the last, shows this to a marked degree. In some individuals it is more prominent than in others. The organism has now received its full number of parts, although with each succeeding molt more segments are

added to the antennae and the twelfth, and particularly the fourteenth, scutum show morphological changes. The twelfth scutum may not be completely differentiated until after the eighth molt while the fourteenth may be variable up to the twelfth molt. Figure 9 shows some of the variations which occur in the fourteenth scutum after the different molts. A number of previous workers, among them Hansen (1903*a*), Bagnall (1914*a*, see fig. 2, pl. 1), Wymore (1924*b*), and Feytaud (1926), noticed variations in the penultimate scutum but evidently did not realize that they were characteristic of certain stages of development. Besides these changes, there is also an increase in the number of setae for at least a few molts after the sixth. Table 3 has been prepared to show some of the more important changes that take place during the first six molts.

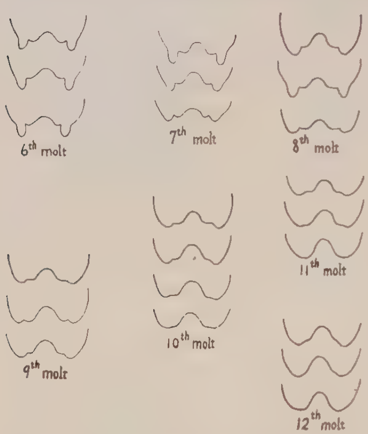

Fig. 9.—Variations that occur in the penultimate scutum of the garden centipede in the sixth to the twelfth molts, inclusive. Note that it may be completely differentiated in the eleventh molt. (× 30.)

ADULTS

The adult individual is very delicate and of a uniform light-cream color, except for the area affected by the digestive tract. The garden centipede is so transparent that the food in the alimentary canal shows through the body wall, and pulsations of the dorsal vessel can be plainly seen through the integument. Pulsations of one kind or another are visible in some specimens from the posterior to the anterior end.

In figure 10, *A*, *B*, and *C* are shown dorsal, lateral, and ventral views of a completely differentiated individual. The lateral and ventral views show a complexity of formations not seen in mounted specimens because the expansions in the integument become completely flattened and lose their identity. In the lateral view the relation of the legs to the dorsal scuta is clearly shown. It is of interest to note that where the scuta are small there are 2 to a single pair of legs. The ventral view shows the genital area, the coxal sacs, and the styli.

Variations in Size.—In reaching full development the animal passes through numerous changes. Up to a certain stage at least, the organism increases in size with each molt. This may explain the great variations in size reported by different investigators. Because the garden centipede

has such a wide distribution, there probably are strains which differ considerably in size. Their length, as reported by some investigators, varied from a range of 2 to 3 mm to a range of 5 to 8 mm. At least three investigators reported the latter range.

The present writer has never seen any individuals as large as the largest reported by others; the largest individuals encountered measured only from 6.5 to 7 mm in length. Many were measured, and it was found that during the early stages the length increased rapidly with each molt up to about the ninth. Thereafter the increase in length was of minor

TABLE 3

IMPORTANT CHANGES IN THE GARDEN CENTIPEDE DURING THE FIRST 7 INSTARS

Instar	Number of antennal segments	Number of pairs of legs	Number of dorsal scuta	Pairs of styli
First	6	6	11*	4
Second	13†	7	10	5
Third	15	8	11	6
Fourth	usually 17	9	13	7
Fifth	usually 19	10	14	8
Sixth	20–24	11	15	9
Seventh	24–27	12	15	10

* Only 10 scuta, if the last scutum is considered to be composed of an anterior and posterior tergite.
† Occasionally there have been 14 segments in the second instar.

proportions, and evidence obtained seemed to indicate that after a time some of the garden centipedes even showed a decrease. Certainly, a point is reached beyond which there is no increase in length, although the individual still continues to molt.

Although not all the same size, when once established the scuta retain their relative size throughout the various stages. Scuta 6, 9, and 12 are the largest, and a careful study shows that the dorsal shields follow a very definite arrangement. Many of the recent workers give the total number of scuta as 14. It appears that they have completely overlooked the first, which is very small, probably because many of them have not been particularly interested in taxonomy. Most of the early workers gave the correct number. Hansen (1903*a*) recognized the first small segment, but did not include it in numbering the scuta. This may have caused some of the later workers to ignore it. But it is important and should be included, for the first pair of legs arises from the first segment.

Relation of Antennal Segments to Molts.—Numerous workers have observed the number of antennal segments in the immature stages. Many of their observations are not the same as those given in table 3. Their inability to determine the expected number of antennal segments for any particular instar and the great variations reported were probably

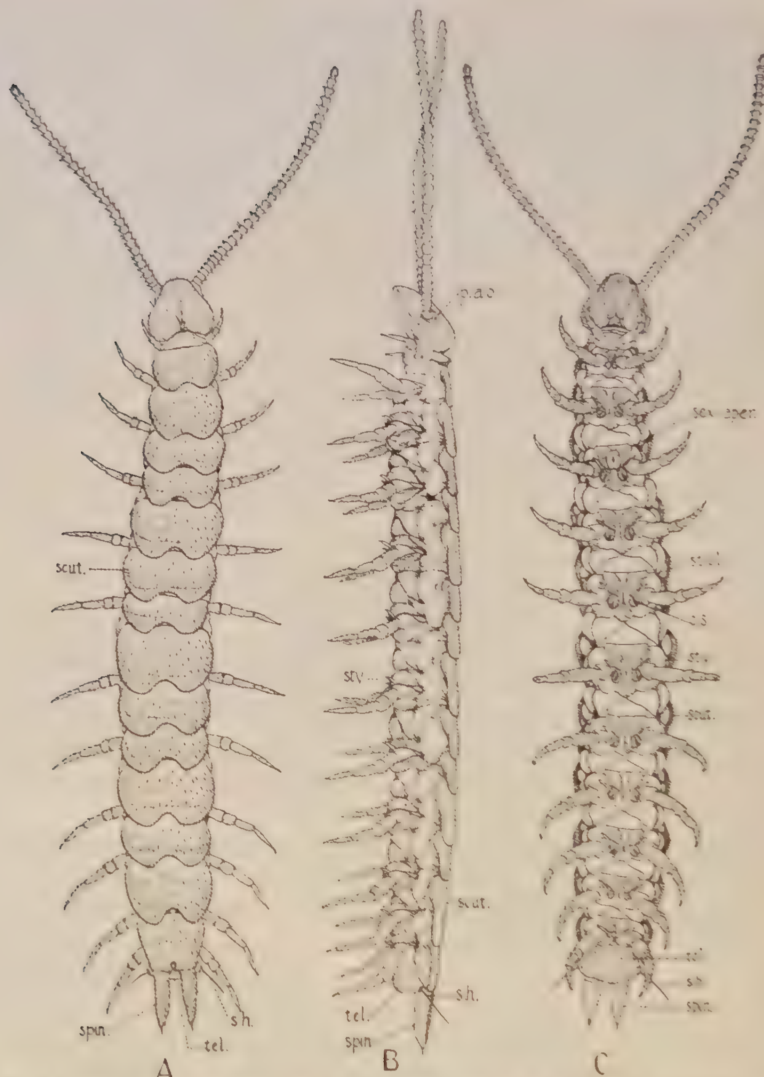

Fig. 10.—Adult garden centipede (× 17): *A*, dorsal; *B*, lateral; *C*, ventral views: *c.s.*, coxal sac; *p.a.o.*, post antennal organ; *sex. aper.*, sexual aperature ♂; *s.h.*, sensory hair; *st. pl.*, sternal plate; *sty.*, stylus; *tel.*, telson; *scut.*, scutum; and *spin.*, spinneret.

due to insufficient material, and to the lack of a method whereby the garden centipede could be kept under constant observation. Some workers who treat the number of antennal segments in the immature forms are: Newport (1845), Latzel (1884*a*), Muir and Kershaw (1909), Williams (1907*a*), Feytaud (1926), Illingworth (1928*a*), Riley (1929), Wymore

(1931), Filinger (1928, 1931*a*), and Verhoeff (1933–34). In studying 200 or more individuals, enough variation was noted to explain the differences reported by most other investigators. As explained below, when parts of the antennae are broken off, they are regenerated a part at a time with each succeeding molt. This is probably the most important factor in explaining large variations.

The variations reported for the number of antennal segments in adults are partially explained in the present life-history study. As a rule, when development was normal the same number of segments was added to each antenna with every molt, although beginning with the third molt an unlike number may appear and continue in succeeding molts even if neither antenna had been recently broken. The number of segments added to the antennae in the later molts under normal conditions varied considerably. The usual number added for each molt was as follows:

Molt	*Segments per molt*
Seventh and eighth	2 or 3
Ninth and tenth	2
Eleventh to fifteenth	1 or 2
Sixteenth and later	1

Complete records beyond the fifteenth molt are not available because etherization after each molt seemed a little too severe, so the segments were counted at longer intervals. Evidence secured on the later stages seems to indicate that some segments are usually added with each molt as long as the organism lives. The greatest number of segments noted in any individual was 60. The count by other investigators for individuals with 12 pairs of legs varied from 18 to 55.

Variation in the number of antennal segments in the same individual may be due to the fact that sections are easily broken off and are then regenerated a part at a time during the following molts. The greatest number of segments is usually regenerated during the first two molts after the break. In the first instar after the one in which an antenna breaks, the broken antenna not only has fewer segments than the normal but also the one next to the base appears slightly elongated (fig. 16, *F*, p. 95), and the apical segment is rounded and not oblong as is the normal terminal segment. If no further accidents occur, the broken antenna tends to catch up with its normal mate.

As early as 1851 Menge noted that the antennae broke off easily but made no observations on their regeneration. Latzel (1884*a*) stated that the antennae were often of different lengths without the shorter one's being injured, and that cases where both antennae were the same length

and had the same number of segments were rather rare. He also noted differences in shape of the terminal joints. Such observations can perhaps be explained by the above study.

Experimental work was conducted which showed that an antenna could be almost completely removed and that with succeeding molts it could catch up with and in some cases even surpass its normal mate. Usually the mutilated antenna gained on its normal mate to a point where it contained only 1 to 3 fewer segments, and then maintained this relation for a number of molts.

Number of Molts.—From a review of the literature it is rather certain that previous workers had no clear conception of the molting characteristics of the garden centipede. Several have stated that the garden centipede molted after it was sexually mature, but failed to give any discussion of the subject. Filinger (1931*a*) gave the most complete account and stated: "A peculiar fact about the garden symphylids is that they continue to molt at intervals throughout their lives; one female molted six times after laying eggs, indicating that sexually mature creatures continue to molt." Wymore (1931) stated that additional molts may occur at various intervals after the garden centipedes have acquired 12 pairs of legs, but did not give any details. Williams (1907*a*) discussed methods of molting and concluded that section of his paper by stating: "Healthy individuals cast at intervals of a few weeks in the laboratory." Verhoeff (1933–34) also observed that the garden centipedes molted after maturity, but was unable to make any accurate observations.

Williams (1907*b*) stated that he had the good fortune to observe a single garden centipede in the process of molting and gave a rather detailed account of what took place. He stated that it was a rather long process which took at least 6 hours. The present writer has observed molting several times, and in all cases the time necessary for shedding the skin was very short (about 15 minutes). Before passing into the molt the organism becomes rather inactive and, as the process begins, appears as if it were dying. The body has a rather rigid appearance, and the legs are pointed posteriorly. It curls its antennae and the antennal segments are pulled close together. As molting continues the garden centipede frees its head from the capsule and by forward propulsions starts to work its way out of the skin. The head is bent downward and, as the animal works forward, the antennae come to lie ventrally on either side of the body. Finally the antennae are freed, and the garden centipede continues to make its way slowly out of the skin. When shedding is almost complete, the propulsions become more active; the antennae are liberated from the sides, and shortly thereafter the organism completely

frees itself. Figure 11 shows a garden centipede in the act of molting, together with some molted skins.

The total number of molts of an individual is not known, but experimental evidence indicates that molting may take place in excess of fifty times. The life-history work is still in progress, and up to the time of preparing this paper, there are individuals that have molted more than forty times. In group cultures which are now nearly four years old, there is little doubt but that most of those still living have passed through 30 or more molts, and the maximum may exceed 50. The exact number of molts in such cultures cannot be accurately determined since different garden centipedes have different molting characteristics, and the number of individuals in any culture does not remain constant because the death of some of them reduces the number from time to time. However, an estimate of the average duration between molts for the mature members of this group is about one to one and one-half months.

Fig. 11.—A garden centipede in the process of molting. Three cast skins are also shown.

Frequency of Molts.—Garden centipedes in the same stage of development show a marked difference in frequency of molting. For example, one may molt in 20 days while another may remain in the same stage for more than 100 days. A number of factors probably influence this, such as food, temperature, sex, injury, and condition of health. Some evidence obtained also indicates that a genetic factor may be involved.

In order to obtain accurate information on molting characteristics it was necessary to rear garden centipedes in individual containers. For the first few molts they behaved much alike, but beginning with the fifth, sixth, and seventh molts the interval between molts became variable, and frequent and less-frequent molters were found. It was further noted that with some individuals after many molts (about the eighteenth to

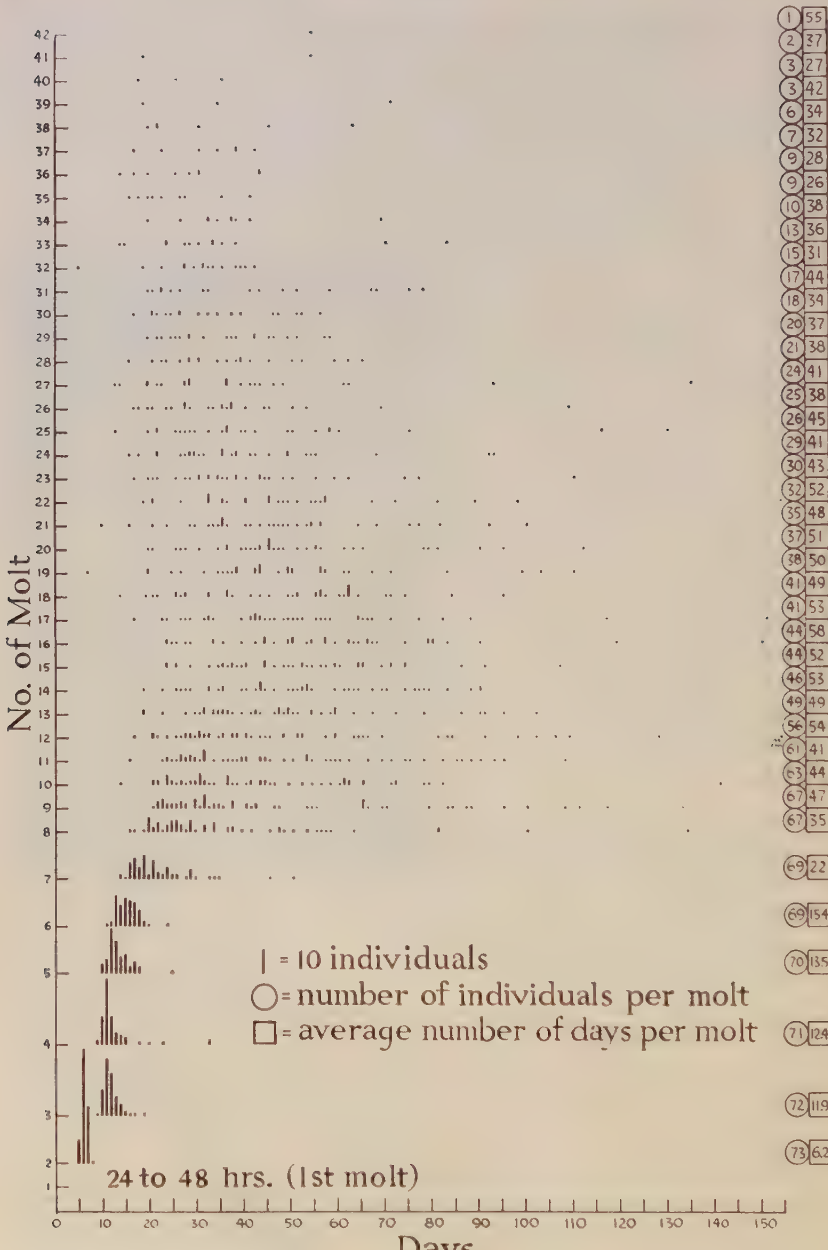

Fig. 12.—Molting variation at room temperature. Since a large percentage of the garden centipedes involved in this study are very slow molters, this chart probably does not show a true picture of a normal group. Note that beginning with the seventh molt, the days between molts show a great variation.

TABLE 4

DAYS BETWEEN MOLTS FOR FREQUENT AND LESS-FREQUENT-MOLTING GARDEN CENTIPEDES IN CULTURES AT ROOM TEMPERATURE AND AT 28°C*

Molt No.	Room-temperature cultures, 21° C										28° C cultures, frequent and less-frequent molters				
	Frequent molters					Less-frequent molters									
	♂	♂	♀	♀	♂	♀	♀	♀	♀	♀	♂	♂	♂	♀	♀
1	2	2	2	1	2	2	2	2	1	1	1	1	1	1	1
2	6	6	6	6	7	5	5	6	5	5	4	4	4	4	5
3	10	16	11	10	12	11	12	12	14	12	5	6	6	7	6
4	11	12	12	11	11	11	10	11	11	11	8	7	8	7	8
5	11	14	12	11	14	13	14	15	13	15	7	7	8	8	7
6	13	18	20	16	13	17	17	15	14	14	10	7	8	14	12
7	17	19	19	21	16	33	29	30	22	25	24	10	14	23	20
8	29	24	38	17	20	46	59	58	48	83	30	13	25	20	34
9	23	24	31	25	32	118	109	101	112	88	24	23	39	15	46
10	21	14	65	27	37	73	79	142	25	50	27	23	38	25	32
11	32	28	32	30	49	83	89	109	75	70	11	20	47	11	37
12	49	29	46	28	42	195	94	67	97	85	26	30	76	44	45
13	34	32	23	32	50	50	96	44	79	57	24	30	79	39	55
14	43	35	23	28	26	91	47	77	65	50	20	30	65	33	65
15	36	37	26	35	45	92	75	66	60	70	46	29	23	40	39
16	43	28	45	40	58	151	80	84	64	69	17	36	28	71	40
17	46	23	44	34	43	152		117	67	83	24	34	22	52	46
18	46	22	63	28	63	63		75	85	63	30	39	26	49	47
19	38	51	27	7	51	57		84	104	66	12	15	11	50	52
20	27	26	46	20	46	21		80	96	79	21	12	13	53	44
21	33	57	42	30	36	21		82	93	49	13	14	11	46	34
22	33	36	37	23	19	27			73	50	15	12	12	59	33
23	39	39	36	33	21				44	111	14	10	14	14	36
24	43	29	27	39	16				36	54	12	15	15	67	41
25	50	22	28	41	27					20	14	12	19	84	90
26	21	28	33	45	20					29	16	11	15	62	48
27	20	23	37	42	28					14	14	12	14		48
28	21	31	24	40	31						17	11	21		36
29	25	23	20	43	43						13	9	18		37
30	27	21	31	35	52						14	10	24		36
31	25	23	69	27	52						15	22	35		
32	43	28	39	32	40						13	17	32		
33	34	29	14	36	24						16	20	21		
34	38	33		39	33						15	20	18		
35	27	16		42	36						15	13	19		
36	20	44		44	26						14	12	20		
37	43	17		35	39						14	15	26		
38	20	22		31							13	16	12		
39	72	19		35							15	14	15		
40	18	26		36							16	23	11		
41	55	19									13	26	20		
42	55										22	12	21		
43											14	12	8		
44											22	22	32		
45											11	18			
46												23			
47												22			
48												22			
49												19			
50												16			

* Age of any individual may be obtained by adding the total days between molts for the garden centipede in question.

the twenty-second), molting again became more frequent. This is indicated in figure 12 and further illustrated in table 4, which also indicates that there is a marked difference in the molting characters of the two sexes.

The data obtained from 71 individual cultures are shown in figure 12. Some of the individuals died from natural causes, while others met with accidents. Even after three years and eight months, however, there were still 8 garden centipedes alive, which makes it impossible to complete the graph. Therefore the figure does not show the true picture of the group, since the 8 individuals still living will continue to molt, and this will cause some slight variation from the results now shown.

While there are frequent and less-frequent-molting garden centipedes, it does not seem possible to place them in two distinct groups because there is a gradation of one into the other. Furthermore, the time between molts for a given individual is not constant. Table 4 shows the intervals between molts for 5 frequent and 5 less-frequent-molting individuals taken from the group used in figure 12. The interval between molts for 5 garden centipedes held in a 28° C incubator is also shown in table 4. This group contains more-frequent and less-frequent molters, and it should be noted that some of the individuals during the latter part of life molted at about a 15-day interval.

From this study it seems that less-frequent molting and long life are linked in some way. The period of molting is apparently a very critical one. Sometimes the garden centipedes appeared to have shed their skins successfully except for completely freeing an antenna or other part of the body. Unless they were aided, death nearly always occurred; in several cases it was noted that the garden centipedes shed their skins at short intervals and then died. Since the process of molting is more or less one of renewal, it may be that molting becomes rapid if there is some disorder which nature is trying to combat. Mutilation does stimulate the rate of molting and the processes of regeneration; the removal of antennae has this effect.

Several experiments were attempted in which different foods were used to determine whether food had any influence on molting. While some evidence was obtained, the results were inconclusive for the most part. Although this point could be rather easily proved from a relative standpoint, only limited work was done because the present writer knows of no exact method of determining the full amount and kind of food consumed. (See section on "Food Habits.")

LENGTH OF LIFE

Under laboratory conditions at least, it is possible for the garden centipede to live for several years. Of about 75 that were hatched from eggs nearly four years ago, 4 are still alive and as active as ever. It is very surprising that such a delicate animal is able to live so long. This fact has been overlooked by most of the workers in this field, although some noted that the garden centipede would live for about a year. Filinger (1931*a*) probably made the closest observations, and he stated that he kept individuals alive in the laboratory for two years and four months. Verhoeff (1933–34) estimated the life of the garden centipede at seven years and stated that with the best of care they would probably live longer. Possibly his estimate was correct although the data from which he obtained it certainly appears faulty. Since as much as a year passed between his observations, it would have been almost impossible to separate the original garden centipedes from their young. The present writer, in comparing individuals about eight months old, was unable to tell accurately the young from the old as far as size was concerned.

TABLE 5

Mortality per 100 Garden Centipedes over a 100-Day Period*

Temperature, ° C	Mortality, first 100 days	Temperature, ° C	Mortality, first 100 days
4.5	1	20.0	5
8.0	6	24.0	38
10.0	3	28.0	52
12.0	3	33.0	70
16.0	7		

* The cultures were maintained at 100; the mortality is equal to the number of centipedes added. Note that the death rate is low until temperatures higher than 20° C are reached.

TEMPERATURE EXPERIMENTS

TEMPERATURE RANGE

An investigation was conducted in which the mortality rate per 100 garden centipedes was observed at different temperatures over a 100-day period. One-hundred individuals were maintained in the cultures so that the mortality for any particular temperature equaled the number of garden centipedes added to the culture. The results obtained are shown in table 5. The death rate at 33°C was very high and fell off rapidly until 20°C was reached. Below 20°C the mortality was low, though fewest deaths occurred at 4.5°C. Some experiments at tempera-

tures below 4.5°C were attempted, but large numbers of individuals were seldom used. The data obtained seemed to indicate that the threshold of development is very close to 2°C, although it might be slightly higher because no feeding was observed at this temperature while at 4.5° C a small amount of feeding occurred and egg deposition took place. The garden centipedes can withstand temperatures lower than 2° C, although they failed to survive at 0° C for any length of time if they had previously been kept at room temperature. However, after a group of about 100 garden centipedes had been held at 4.5° C for nearly nine months, 4 of them survived 0° C for eight months.

At 4.5° C the garden centipedes were very sluggish, at 10° C they moved rather slowly, but above 12° C they appeared quite active. If activity and low mortality can be used as a basis for determining optimum temperature, the results indicate that this lies between 12° and 20° C. This could probably be narrowed down to 16° to 20° C, although figures 13 and 14 plainly show that they are stimulated to greater activity at higher temperatures.

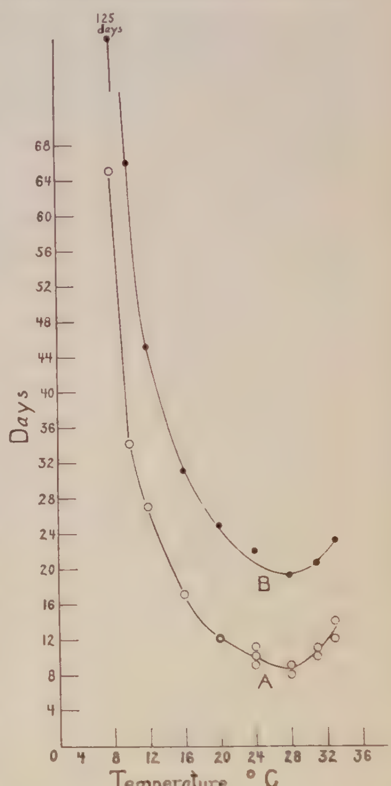

Fig. 13.—Curve *A* represents the number of days before molting begins. Groups of 100 individuals, taken from lettuce leaves and considered to be in the feeding phase, were used for the experiment. Curve *B* represents the number of days before 50 per cent of the garden centipedes molt. Note how closely the two curves follow each other. The most rapid molting takes place at 28° C.

At higher temperatures the garden centipede actually seems to decrease somewhat in size, and young reared at such temperatures appear to be slightly smaller on the average than those held at room temperature. However, in one group of 12 individuals reared at 28° C, 10 were still alive after twenty-four months and as late as thirty-four months 4 were still living. This gives strong evidence that the garden centipede can adapt itself to rather high temperatures.

The thermal death point lies close to 37°C. A group of garden centipedes previously held at 28°C for 24 hours died in less than 1 day at this

temperature. This is not surprising since they are soil-inhabiting organisms and have little opportunity or need to resist high temperatures. Garden centipedes subjected to gradual changes in temperature can withstand greater variations than can those exposed to very sudden changes. The absolute maximum and minimum temperatures at which they can survive are dependent upon the hardening process to which they have previously been exposed.

EFFECT OF TEMPERATURE ON MOLTING

Cultures were held at various temperatures in order to determine the effect of temperatures on molting. Each culture, containing 100 large garden centipedes, was divided into two parts of 50 each. A supply culture was also maintained to furnish replacements in case any of the garden centipedes in the main cultures died. By so doing the numbers in the cultures were kept at 100. In making replacements it was impossible to place an individual in the culture at the same stage of development as the one that had died, but probably the law of averages would take care of this discrepancy. Garden centipedes used in the experiment were obtained from the lettuce leaves in the storage cultures. Such individuals were considered to be in a feeding phase. At this time apparently molting rarely occurs, so this period is referred to as the feeding, or premolting, period. When the temperature is sufficiently high, a considerable amount of lettuce is eaten before molting begins. The length of the premolting period is also influenced by temperature. The amount of food consumed in the initial period of heavy feeding is shown in figure 20 under "Food Habits."

If the periods at which molting begins are plotted (fig. 13, *A*), it is found that at the lower temperatures the premolting period is lengthened, but becomes shorter as the temperature rises until a certain point is reached which lies near 28°C. At this point the period begins to lengthen again. The time necessary for 50 per cent of the garden centipedes to molt at the different temperatures is shown in figure 13, *B*. Note that this curve closely follows that which shows the time when molting began. No temperature higher than 33°C was used since this approximates the limit beyond which the garden centipedes do not thrive. Even at this temperature, after about 20 days, they begin to die off rather rapidly, possibly most frequently during the molting period. If this is so, the replacements would not give a true picture of the actual molting behavior at this or higher temperatures. It should be stated that some garden centipedes have lived at 33° C for months, which indicates that many of them can adapt themselves to this high temperature.

At 4.5° ± 0.5°C it was several months before any garden centipedes molted. In the supply culture kept for replacements one molted at the end of 160 days, and later two more shed their skins. In the regular cul-

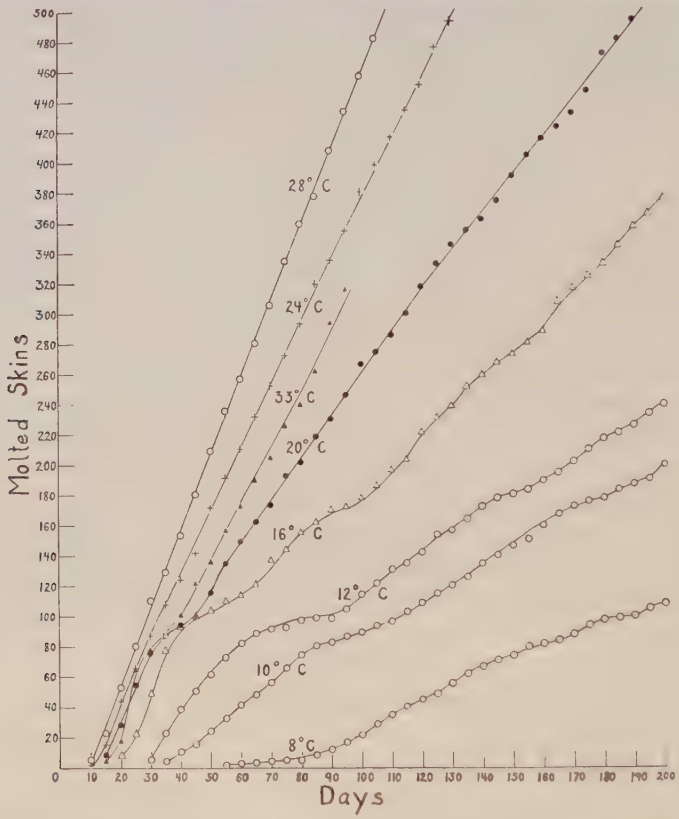

Fig. 14.—Rate of molting per 100 individuals at different temperatures, with the garden centipedes considered in the feeding phase at the beginning of the experiment. Total molts are shown for 5-day intervals. Note that molting is most rapid at 28° C, and at 33° is retarded somewhat, falling between that of 20° and 24°. At 28°, data are based on 200 individuals up to 80 days, and 150 thereafter; at 24°, on 300 individuals; at 20°, on 200 individuals up to 30 days, and 100 thereafter. In all other cases data are based on the molting activity of 100 individuals.

tures the first garden centipede molted after 214 days and between that time and 252 days 11 more individuals molted.

Figure 14 shows curves for the total molts obtained at 5-day intervals. It shows that 24° and 28°C give the greatest number of molts and that temperatures either above or below these give fewer. Note that the rate of molting for those individuals held at 33°C falls between that of 20°

and 24°C. At higher temperatures the rate of molting can be plotted almost in a straight line, but this does not hold true at lower temperatures. This is probably because the garden centipedes are in the feeding

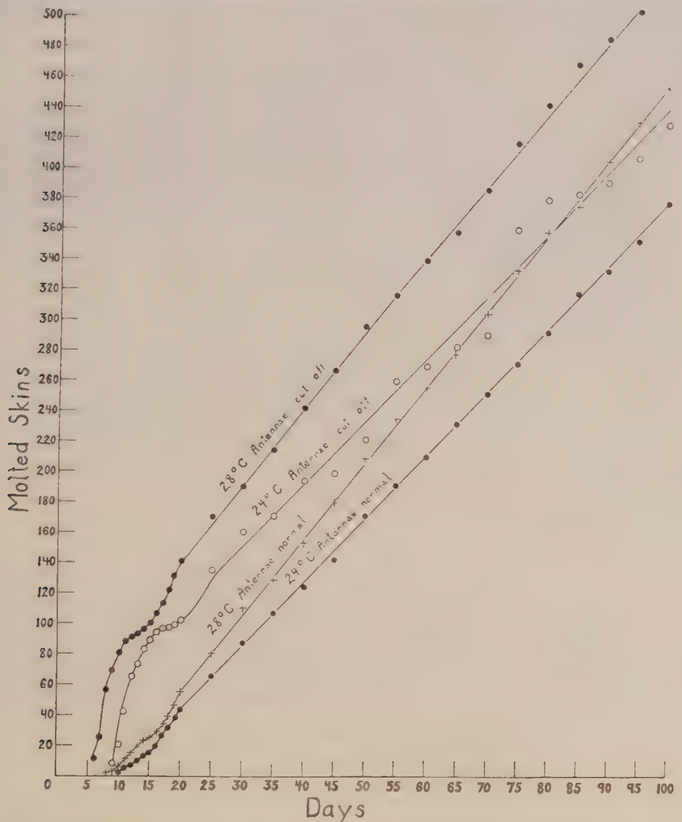

Fig. 15.—Stimulating effect of the removal of antennae on molting per 100 individuals. Total molts are shown daily for the first 20 days, and at 5-day intervals thereafter. Individuals whose antennae were removed passed through the first molt in a remarkably short time. Observe that a lag occurs before the second molt begins, and that the rate of molting of the mutilated forms thereafter tends to parallel that of the normal groups, which are the same as those in figure 14. Curve labeled "28° C antennae cut off" based on activity of 100 individuals; that for 24° based on 100 individuals for the first 65 days, and thereafter on 50. All garden centipedes at the beginning of the experiment were considered to be in the feeding phase.

stage to begin with, and there is a tendency for them to molt more or less together. After molting they pass into another feeding stage, in which molting apparently does not occur. At higher temperatures these periods are relatively short, and, since the molts are shown for only 5-day periods, there is a tendency to smooth out the curve. This effect is also

brought about by the fact that at higher temperatures large numbers were used, and in taking the average molts per 100 centipedes, variations are almost entirely obliterated. At lower temperatures the process is much drawn out, so that the molting and nonmolting phases give the curve an undulating appearance. This is rather readily understood when one considers that at 28° C a garden centipede molts on an average of every 22 days, while at 10° C molting takes place every 100 days.

The removal of antennae greatly stimulates the rate of molting. This is considered at this time because there is also a temperature relation here. The garden centipedes were etherized and the antennae severed with a needle, the point of which was flattened and sharpened to a cutting edge. One hundred such individuals were kept at 24° and 28°C, respectively, together with cultures for replacements. The shock of removing the antennae was so severe in some cases that the garden centipedes did not recover, which necessitated numerous replacements at first. Most of these were made before molting began, so they need not be further considered. In spite of the fact that the garden centipedes were in the feeding phase at the time the antennae were removed, they failed to feed to any extent after the operation. Nevertheless, in a very short time they began to molt, and in a few days most of them had shed their skins. Molting was more frequent at 28° than at 24°C. As individuals passed through molts, there was an increase in feeding which became very marked by the time the majority had molted. The rate of molting when compared with that of normal individuals under similar temperature conditions is most striking. The majority of the individuals in the group which had their antennae removed molted before those in a normal group had begun. The stimulating effect of mutilation is not permanent, however, and is lost by the end of the second molt. From this point the molting rate is about the same for both. This is clearly shown in figure 15, and it should be noted that after the period of most frequent molting there is a lag, followed by an increase in molting rate. The second increase does not compare with the initial frequent molting.

EXTERNAL ANATOMY

HEAD

The head of the garden centipede is more or less heart-shaped and fairly well covered with short hairs. The mouth parts are of the chewing type and have been described by many workers. Some of the more important papers that consider them and their structure are: Muhr (1882), Wood-Mason (1883), Latzel (1884*a*), Grassi (1886), Hansen (1903*a*), Voges (1920), Becker (1922) (*Scolopendrella vulgaris*), Attems (1926), Adensamer (1926), Filinger (1931*a*), Pflugfelder (1932), and Verhoeff

(1933–34). Since the mouth parts are well treated by these investigators, they will not be discussed here. An extensive review is given by Verhoeff (1933–34).

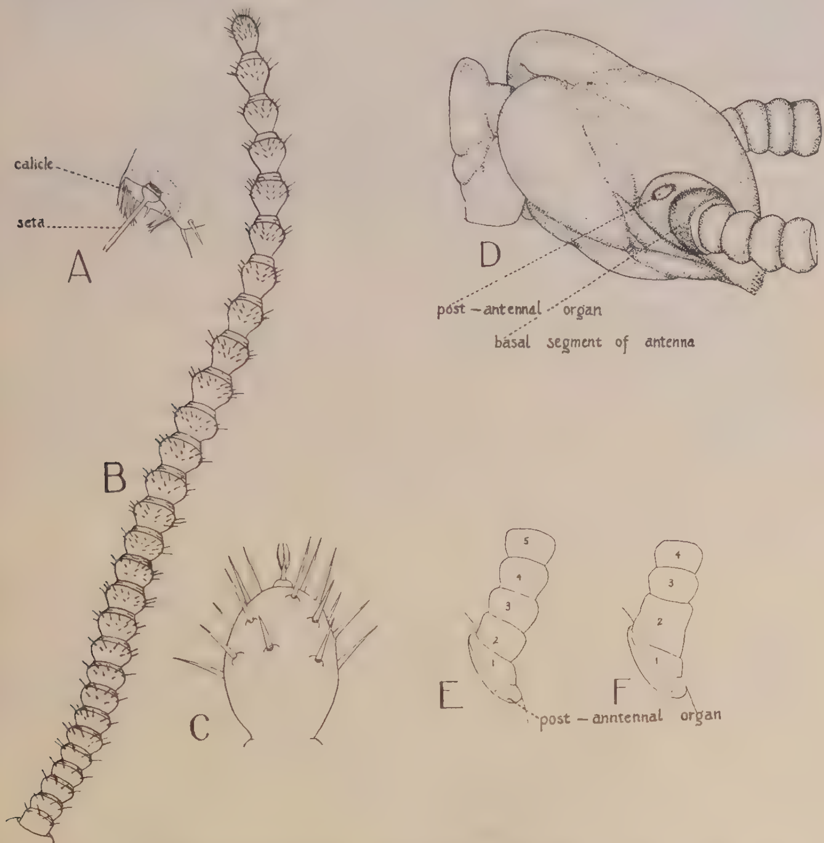

Fig. 16.—*A*, Posterior sensory hair of the garden centipede (× 225); note the bulbous base of the sensory seta. *B*, Antenna (× 55). *C*, Terminal segment of antenna (× 250) showing peculiar sense organ at the apical end; drawn from a prepared slide. *D*, Head (× 70) showing relation of post-antennal organ to basal segment of antenna. *E*, Proximal segments of a normal antenna (× 65). *F*, Proximal segments of an antenna (× 65) where most of the segments were removed before molting; note the elongated second segment, a condition that occurs whenever many segments are cut off.

The garden centipedes are eyeless and apparently feel their way about with their long, many-jointed antennae (fig. 16, *B*). Since these are described elsewhere (p. 81), only their peculiar sense organs (fig. 16, *C*), one of which is located on each terminal joint, are mentioned here. These were discovered by Hansen (1903*a*), who described each organ as consisting of a stalk which is either short or rather long, often

gradually increasing in thickness outwards, and from whose end originate four fine branches which are slightly convex outwards, subparallel or slightly diverging, and always united by a very thin, clear membrane. Since his time these organs have been discussed by several other authors.

Post-Antennal Organ.—Near the base of each antenna (fig. 16, *D*) is located a structure which has the superficial appearance of an ocellus. It shows up most clearly in live specimens when viewed from the side, although it is easily seen from the dorsal aspect. It appears slightly convex, more or less oblong in shape, and when the light falls from certain directions, it looks pearly in color. If seen on live specimens it appears to be situated on a separate sclerite, but on prepared slides this sclerite appears to be continuous with the basal antennal segment, although there is some little evidence of a suture between.

These organs have been observed by many investigators who have suggested their possible function. The most complete work is that of Pflugfelder (1933). In his study he called attention to the difficulty in fixing the brain. He was able, however, to work out the finer histological structure in detail. The nervous tissue which supplies the structure arises from the tritocerebrum—an indication that it is a post-antennal organ. He also found a great similarity between the post-antennal organs of Symphyla, Diplopoda, and Chilopoda, those of Symphyla being the most complicated. The sense cells are always divided into distal and proximal cell portions. In Symphyla the distal portion has the most complicated structure consisting of 5 to 16 rodlike differentiations in the center of which runs a neurofibrilla. The proximal portion is connected by a short process with ganglion cells, and is therefore a primary sense cell.

Pflugfelder also stated that these findings contradict the views of earlier authors that these post-antennal organs are ocelli, chemoreceptors, or sense organs for the reception of physical changes in the earth or air. The presence of the portion capable of oscillation indicates an organ for the perception of vibration, perhaps also of noise and sound.

Other workers who have considered the post-antennal organ are Grassi (1886), Schmidt (1895*a*), Attems (1926), Becker (1922), and Verhoeff (1933–34).

Stigma.—A single pair of stigmas are found just below the post-antennal organs.

BODY SEGMENTS

Since body segments are treated under the section on "Life History," a discussion will be omitted here except to say that there are apparently 12 segments and a telson. Dorsally there are 15 scuta, and the relation of these to the legs and body segments is clearly shown in figure 10, *B*.

Legs.—The mature garden centipede has 12 pairs of legs. Each leg terminates in a pair of claws. The first pair of legs is 4-segmented and is smaller than the others, which are 5-segmented. The correct terminology of the precise segmentation of the leg is a debatable question (fig. 17, *B*). Wood-Mason (1879) reached the conclusion that the legs of

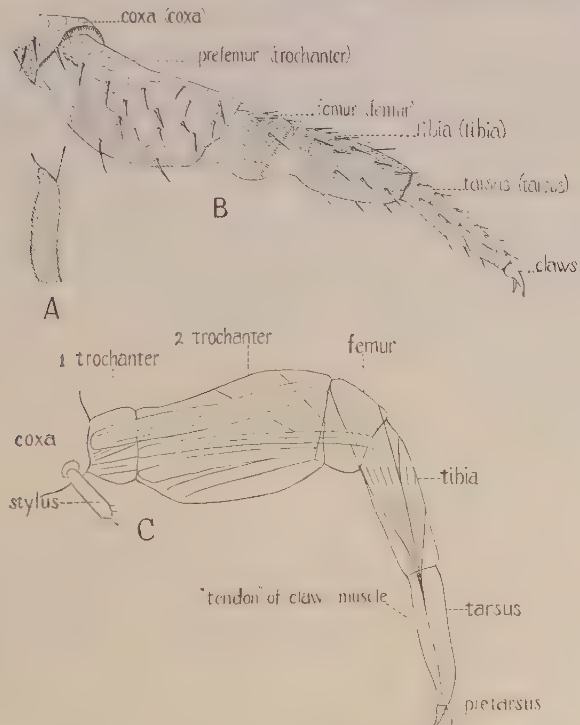

Fig. 17.—*A*, Stylus (× 250). *B*, Leg (× 100); terminology of the leg segments: without parentheses, according to Verhoeff; with parentheses, according to Ewing. Note the integumental design on the coxa and prefemur. Somewhat similar markings are present on the integument over various parts of the body. Drawn from a prepared slide. *C*, One leg of the last pair (× 120). (Drawn and labeled by R. E. Snodgrass.)

symphylans were exopodites and that the appendages to the legs were nothing more than functionless rudiments, which could be considered as endopodites. This, he pointed out, was just the reverse of what occurred in *Machilis* where the appendages to the legs were to the outside and corresponded to the exopodite, while the leg represented the endopodite. Imms (1908) designated the appendages of the legs as exopodites, which is just the reverse of the belief of Wood-Mason.

The names given by a number of workers to the various segments of

the 5-segmented leg are: coxa, prefemur, femur, tibia, and tarsus. Williams (1907*a*) pointed out that most workers considered the first movable segment as the coxa, but Hansen (1903*a*) and Feytaud (1926) named the movable segments trochanter, femur, tibia, metatarsus, and tarsus, the latter terminating in a pretarsus. Hansen also stated that the coxa could easily be seen as a separate portion of the skeleton on the lower surface of the trunk on a specimen cleared with caustic potash. Tillyard (1931) reported that the symphylan leg consisted of but 4 segments—coxa, trochanter, femur, and tibiotarsus. What many workers called the coxa he considered the subcoxa.

After studying the muscle attachments and articulations, Ewing (1928) reached the conclusion that the 5 movable segments should be named coxa, trochanter, femur, tibia, and tarsus. Using his terminology, the trochanter is the very large and the femur the much-reduced segment, and according to his interpretation the femur is not present in the first pair of legs.

Snodgrass[12] writes:

> In reëxamining the legs, I find that it is in the last pair that the structure is most evident which has given me the idea of the presence of a small segment between the stylus-bearing coxa (blended with the sternum) and the large proximal segment (*2 Tr*) [second trochanter]. This small segment, which I have called first trochanter (*1 Tr*), is very inconspicuous if present at all in the more anterior legs.

In living specimens the present writer believes that the small segment mentioned by Snodgrass is discernible in all but the first pair of legs, but in mounted material it is obliterated (see fig. 17, *C*).

Styli.—The first of the ventral appendages to be considered are the styli (figs. 10, *sty.*, and 17, *A*). These small structures, located near the base of the third to the last pair of legs, have been known under various names, such as rudimentary legs, parapods, and exopodites. Haase (1889) spoke of them as "abdominal griffel" and stated that they should not be considered as rudimentary legs but as secondary paired hair structures, which have developed from purely sensory to locomotor organs. Schmidt (1895*a*) disagreed with Haase. In regard to their phylogenetic development, Schmidt stated that a fusing of the posterior body segments into double segments had gone further: the 2 pairs of legs were fused at the coxa, and each posterior pair of legs was reduced to a pair of parapods. Williams (1907*b*) also believed that the styli were rudimentary legs, while Imms (1908) spoke of them as exopodites, as did Ribaut (1931). Daiber (1913) considered them modified spurs, or processes of the coxal joints.

[12] Snodgrass, R. E. In letter to author, April 11, 1936.

Ewing (1928) did not believe that the styli were true appendages. He stated:

> The so-called coxal appendages in the Pauropoda, Symphyla, and Thysanura are not true appendages and have no muscle fibers attaching to them. They are probably not homologous among themselves. Some may represent structures analogous, or possibly even homologous, with either the epipods or the exopods of Crustacea.

Some of the previous investigators believed that the styli were sensory in function, while others believed that they served in locomotion. Since they are so small, it seems almost impossible that they can be of much service to the garden centipede in moving about.

Coxal Sacs.—The coxal sacs occur on the ventral surface of the organism just posterior to and slightly towards the medial line from the coxa. Many individuals were examined, including anesthetized ones and prepared specimens mounted in modified Berlese medium to which iodine had been added. No evidence of coxal sacs was found in the case of the first pair of legs. All other pairs showed these organs or evidence of them. Those associated with the second and eleventh pairs of legs appeared to be slightly less than half the size of the rest, with the exception of those present on the last segment. The latter were only slightly larger than the diameter of the styli of that segment, or about one-half the size of those just anterior to them. Since the so-called "coxal organs" of the second, eleventh, and twelfth pairs of legs are smaller, and may possibly be of a different structure, they may represent rudiments of coxal organs. This seems to be particularly true of the last pair because, in mounted specimens examined, they appeared to be nothing more than small plates with several rather strong spines arising from them.

In examining anesthetized specimens, the completely developed sacs at first glance seem to stand out as pearly, glistening structures, but on closer examination one can observe a V-shaped fissure cutting diagonally through the clear, raised portion. This is due to the fact that the eversible sacs are not fully extended. The raised, clear area is partly surrounded by rather strong spines, arranged more or less parallel to the fissure, which extends obliquely and anteriorly from the outside margin towards the median line of the body. The V-shaped depressions of a pair of coxal sacs tend to converge anteriorly (fig. 18, *coxal sac*). Figure 10, *C* is a ventral view of a garden centipede showing the arrangement and relative size of the coxal sacs. Figure 18, *C* illustrates the type of structures found on the second segment while figure 18, *D* shows the same for the last 2 segments.

Investigators have not agreed on the number of coxal sacs as above described. Many of them noted rudimentary sacs on the second and elev-

enth segments but those of the twelfth segment were overlooked in must cases. The number of fully developed sacs reported by different workers varied from 8 to 11. This variation can be accounted for, in part, by the interpretation given to the rudimentary sacs, but in some cases it was

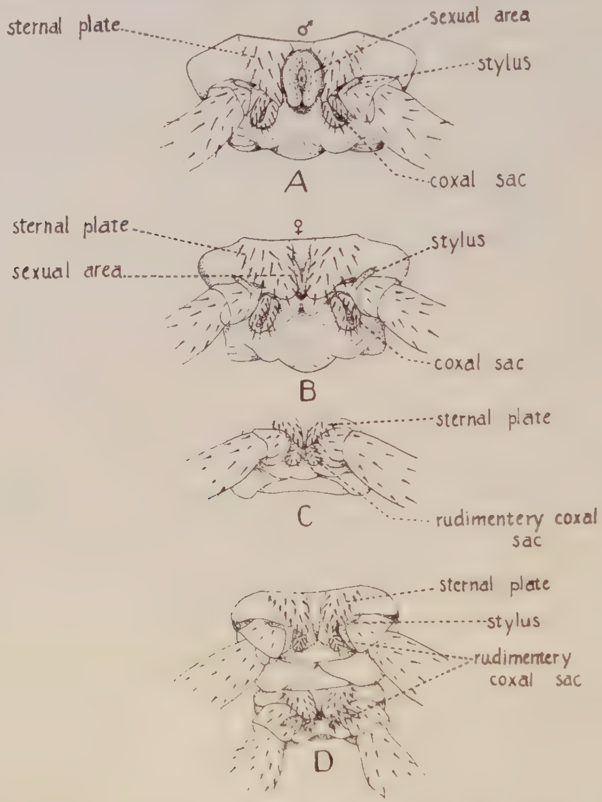

Fig. 18.—*A*, External genital area of male garden centipede; *B*, external genital area of female; *C*, structures associated with second pair of legs; *D*, structures associated with eleventh and twelfth pairs of legs. (× 55.)

probably due to faulty observations. Some of the variations reported may have been due to species or generic differences. Verhoeff (1933–34) stated that from his own observations there were individuals to be found which did not have coxal sacs on the eleventh segment, but he was not sure whether he was dealing here with a species difference or an individual or local variation. Ribaut (1931), in this regard, called attention to the fact that there was a generic variation in Symphyla, and stated that the last 3 pairs of legs in *Scolopendrella, Symphylella,* and *Sym-*

phylellopsis lacked coxal sacs, while in *Symphylelline, Geophilella, Ribautiella, Scutigerella,* and *Hanseniella* they were lacking on only the last 2.

Wood-Mason (1883), Grassi (1886), and Ribaut (1931) agree with the present writer that there are only 8 fully developed pairs of coxal sacs occurring at the bases of legs 3 to 10, inclusive. Haase (1889), Schmidt (1895*a*), Daiber (1913), Friedel (1928), and Verhoeff (1933–34) believed that there were 9 pairs. Williams (1907*a*), Feytaud (1926), and Attems (1926) stated that there were 10 pairs, while Packard (1903) listed 11.

Although a number of workers have suggested the function of the coxal sacs, nothing is definitely known in this regard. Wood-Mason (1883) thought that they might be excretory in nature. Haase (1889) believed that they supplemented the "tracheal" system (see p. 103) and functioned as sort of blood gills, while Friedel (1928) concluded that they might also serve as the locus of the sense of moisture. Williams (1907*a*) also believed that they were accessory to the "tracheal" system, and stated that they might serve as respiratory organs by allowing the passage of oxygen through their exceedingly thin walls. Verhoeff (1933–34) was of this same opinion. Among the arthropods studied by Haase (1889), he noticed that the more reduced the "tracheal" system, the better developed were the coxal sacs. Because, in the garden centipede, the coxal sacs begin at about the point where the "tracheae" end, it seems that this would certainly tend to indicate that the sacs are respiratory in function.

Sex Characters.—The sex ratio is approximately 1 to 1. Of 1,532 large individuals collected at random, 776 were females and 756 were males.

Differentiation of the sexes of the garden centipede has led to considerable confusion, particularly in regard to distinguishing them on the basis of external characters. Grassi (1886) was the first to do any extensive work on the reproductive system. His work was rather accurate, according to Schmidt (1895*a*), who further advanced the knowledge of this organ system. Schmidt gave a very complete account of both the male and the female reproductive organs, including the external characters. His is the most outstanding work which has been published up to the present time.

The characters which separate the sexes can be seen in cleared, mounted specimens and also in living material if properly illuminated. These characters as seen in living material are shown in figure 18, *A* and *B*. Note that the distinguishing features of the male are more prominent, and the sternal plates are very different in the two sexes. Three recent

workers, Filinger (1931*a*), Ribaut (1931), and Larrieu (1934), observed these characters but confused the sexes.

It has been suggested that the females are larger than the males. For example, Filinger (1931*a*) stated that in mature specimens the males are generally smaller than the females. Yet, since he confused the sexes, his observations would show that the males are larger. From the preponderance of evidence, the present writer feels that the latter is incorrect. Size cannot be used with accuracy in separating the sexes. Although the females are probably larger than the males, the difference is too small to be relied upon.

Sensory Hairs.—A pair of very noticeable sensory hairs arises from bulbous bases, one on either side at the posterior end of the garden centipede (figs. 10 *s.h.*, and 16, *A*).

Spinnerets.—The spinnerets, situated at the posterior end of the body, may be considered as modified cerci. Each spinneret has a separate silk gland; a duct leads out and opens at the tip of the spinneret. The garden centipede apparently secretes the silk-producing material with great ease. When examining etherized specimens it is not uncommon to see globules of this material protruding from the tips of the cerci. When the globules are fairly large they are rather opaque, glistening, and tinged with blue. The material is of a jellylike consistency and adheres to an object with the tenacity of glue.

In active specimens, the touching of the tips of the spinnerets with a camel's-hair brush will cause them to start spinning a web, and if the brush is raised quickly, the garden centipedes can be lifted from the substratum. In fact, this is the method used in gathering and transferring individuals from one container to another without injuring them in the least.

Fabre (1855) noted the spinnerets in *Scolopendrella*, but took them to be rudiments of legs that terminated the body of *Cryptops*, and thought them young of this animal. Chalande (1889) described the spinnerets in considerable detail. Haase (1889) thought that they corresponded to the cerci in insects, while Schmidt (1895*a*) believed that the spinnerets were homologous to running legs, and stated that in the embryological development they were laid down as such. Daiber (1913) believed that the spinning glands probably belonged to the same category as the coxal glands. Williams (1907*a*) thought that the spinning glands were modified dermal glands.

Williams (1907*b*), Riley (1929), McDaniel (1931), Filinger (1931*a*), and Miles and Cohen (1935) believed that the garden centipedes lined their runways with silken threads. The present writer cannot substan-

tiate this and believes that what some of the investigators thought might be threads were in reality fungus mycelia. Wymore (1931) says:

> It is claimed by some students that the runways are lined with webs, which thus serve as a "life line" so that the centipedes may safely retrace their steps, and that eggs are often covered with webbing. The writer's observations have been that very few webs appear in the natural runways or on the eggs as found in the fields, but that after keeping the centipedes or the eggs in a moist container for a few days, a network of what seems to be webs appears all over the surface of the soil and the eggs. However, a microscopic examination showed that the majority of these web-like structures were mycelium threads of some fungus, which might be mistaken for a web.

The true function of the spinnerets is not known. Wymore (1931) suggested that the web spun might serve as an anchorage, while Verhoeff (1933–34) believed that the spinnerets might be used in escaping danger. He observed that when a garden centipede was attacked, for example by a carabid larva, it sprang immediately to the side, and if the attack was repeated, it could let itself fall into any passage or fissure and hang there by its threads as by a rope. Because there is a tendency for them to secrete the silk-forming material when they are disturbed, the spinnerets may function for protection. Possibly, also, the secretion may aid the garden centipede in molting by cementing the skin to the substratum.

INTERNAL ANATOMY

Internal anatomy, although it was not dealt with in the present investigation, has been studied by numerous authors. Some of the more important works on the subject are those of Menge (1851), Grassi (1886), Schmidt (1895*a*), Larrieu (1934), and Verhoeff (1933–34). Verhoeff brings the information up to date.

A short discussion will be given of the respiratory organs. Symphyla have only 2 stigmas. These are located on each side of the head posterior to the insertion of the antennae under the post-antennal organs. From each stigma arises a tube with a number of branches. The entire system is restricted to the head and the first 3 body segments. The ramifications of the so-called "tracheae" in *Scolopendrella nivea* (Scop.) are shown in figure 19, which has been taken from Haase (1885). The principal "tracheae" lack spiral thickenings, or intimae, as noted by Haase (1883, 1885), Ripper (1931), and Verhoeff (1933–34). Posterior to the third body segment the coxal sacs may function as organs of respiration.

Some of the early workers experienced trouble in distinguishing the "tracheal" system. Ryder (1880) and Wood-Mason (1883) mistook the skeletal arches for "tracheae," although Menge (1851) showed that they

were structural supports. It should be stated that Wood-Mason observed "tracheae" in the head. Haase (1883, 1885) studied the "tracheal" system carefully and gave a good description of it. Among others who gave correct interpretations of it were Latzel (1884*a*), Daiber (1913), Ripper (1931), and Verhoeff (1933–34).

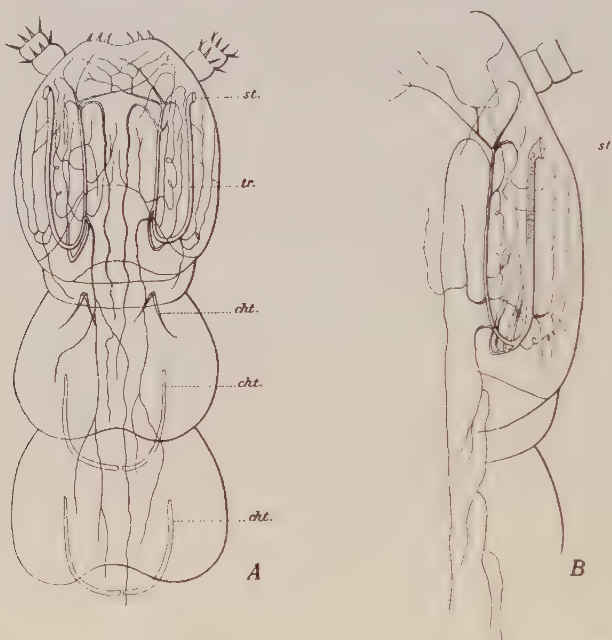

Fig. 19.—"Tracheal" system of *Scolopendrella nivea* (Scop.) as seen from above. *A* shows the entire system, while *B* is a greatly enlarged drawing of the right side; *st.*, stigma; *tr.*, tracheae; *cht.*, skeletal structures. (After Haase, 1885.)

FOOD HABITS

Many of the early workers thought that the garden centipede was predaceous. Newport (1845) stated that they ran with great celerity, from which he was inclined to regard them as carnivorous. Latzel (1884*a*) also believed that their great agility, the structure of their mouth parts, and their straight digestive tract indicated an animal diet composed largely of arthropods. Williams (1907*a*) cast some doubt on their carnivorous habits, but in his summary he stated that *Scutigerella* was probably an animal feeder. He further added (1907*b*) that the appearance of sections of the intestine and the abundance of Infusoria, Rotifera, and many other minute forms where *Scutigerella* thrived best, tended to support this view.

On the other hand, Lucas (1871), referring to *Scolopendrella notacantha* (Gerv.), stated that its nourishment without doubt consisted of debris of organized matter, especially vegetable substance. Ryder (1880), in discussing *Scutigerella gratiae,* stated that the portion of the intestine in front of the rectum was dilated; this was especially noticeable where that part of the alimentary canal was usually filled with the remains of undigested vegetable food.

Feytaud (1926) and Larrieu (1934) believed that the garden centipedes were primarily vegetable feeders, although they believed they were carnivorous at times.

Some investigators believed that the symphylans were humus feeders. Thompson (1924), speaking of *Scolopendrellopsis subnuda, Symphylella delicatula,* and *Symphylella vulgaris,* stated that they were relatively inactive, not very responsive to external stimuli, and that, as far as could be ascertained, were exclusively humus feeders. Almeida (1930) kept the garden centipede, *Scutigerella immaculata,* alive for five months in soil gathered in an orchard. Because the garden centipedes lived for such a long period, he concluded that it was rather certain that the humus and even the subterranean microfauna must have contributed to keep the animals alive. Riley (1929) reported the symphylans as damaging cultivated crops in greenhouses. When the crops were planted in the fall, he believed that they migrated to the surface soil to feed, but that during the summer their food was largely decaying organic matter. Filinger (1931*b*) also believed that they fed on decaying organic matter as well as on living vegetable tissue.

Several workers have tried keeping the garden centipede under varying degrees of sterilization and noting its length of life. Williams (1907*a*) baked the soil in some of the cultures and found that death occurred more rapidly than in the unsterilized containers. Friedel (1928) found that in a tube containing burned and sterilized clay with sufficient moisture *Scutigerella* lived more than three months. On sterilized tile he kept them alive for 35 days. In sterilized earth containing humus they remained alive for three and one-half months. He noted that under these conditions they became smaller, thinner, and more transparent. Wymore (1924*a*) reported that he kept garden centipedes alive in a small tin box containing moist earth in the absence of succulent material as long as nine or ten months.

In the present investigation no attempt was made to rear the garden centipedes under sterile conditions for it would be of little value to sterilize the substratum unless the organism itself and all materials added were also sterile.

Many interesting observations were made, however, on the feeding habits of the garden centipede. Lettuce was generally used as food, although several experiments were conducted in which carrots formed the basic diet. No evidence was obtained that the garden centipedes are predaceous although they were observed to feed on animal material. Verhoeff (1933–34) stated that their mouth parts do not lead one to believe they are predaceous, nor was he able to observe any predaceous habits, but noted them eating crumbs, flesh of apple, and leaves.

In a number of cases the garden centipedes were noted feeding on their own dead and in one case an individual was observed feeding on one that was severely injured. Their feeding is certainly not confined to succulent plant material, although the present writer believes that this is the preferred diet. They evidently feed on many lower forms of plant life, for groups of garden centipedes have been observed to eat heavily of compressed yeast. Also a number have been placed in rearing dishes whose surfaces were covered with a growth of unicellular green algae which disappeared after some time. Probably the garden centipede ate it, although its disappearance might have been due to their waste products. The latter explanation, however, hardly seems possible because, if the garden centipedes are removed and the rearing dish kept moist, the growth returns. Since no marked accumulation of feces has been found in containers in which garden centipedes have been kept for over two years, it seems reasonable to assume that most of the feces are reduced by other organisms such as fungi and bacteria, and these are in part eaten by the garden centipede. At any rate, it is very noticeable that molds rarely grow in the garden-centipede cultures which receive proper care. To what degree the garden centipedes feed on lower plant life in the absence of succulent tissue is not known, since it is nearly impossible to get accurate data on what happens to the microflora that arises from the substratum. Although some workers believe that they feed on humus, the present writer believes that they are eating the saprophytic growth that arises from it and not the humus itself.

Carrots were used as a successful food in 12 individual cultures, although, judging from the molting frequency of this small group, carrot did not seem to equal lettuce as a food supply. It was also more difficult to handle.

Under the heading "Effects of Temperature on Molting," it has been suggested that the garden centipede has feeding and nonfeeding phases and that a relation is shown between the feeding phase and the molting phase. An attempt was made to determine what relation exists between feeding and temperature. At the time much of this work was done, con-

stant temperatures were difficult to maintain in the chambers then available, and for this reason some of the early results obtained were not very reliable. It was also difficult to account for the natural gain or loss of the lettuce used. The investigation was carried out as follows: garden centipedes were obtained from the lettuce leaves in the storage cultures and so were considered to be in the feeding phase. In this part of the investigation two cultures containing 50 garden centipedes each were run at the different temperatures. Since the larger garden centipedes weigh about 1 milligram each, the total weight for each culture was about 45 to 50 milligrams. The pieces of lettuce used for food were weighed before placing them in the cultures. Two checks were always run to determine the natural loss of weight of the plant. The bits of lettuce used for this purpose, when possible, were taken from the same leaf that was fed the garden centipedes and were placed in the same type of rearing dishes. At first the lettuce was replaced every day, but, as feeding became less, it was changed only every other day, and at the lower temperatures the interval was extended even longer. At every change the garden centipedes and the lettuce were weighed.

Because temperatures fluctuated considerably, it seems unwise to try to compare them all, but some statements can be made. When the garden centipedes are taken from the storage cultures, they have ravenous appetites. During the first 24 hours, at the higher temperatures, they eat about three times their own weight. During the second 24 hours they consume more than twice their weight; thereafter the amount falls off rapidly down to a certain point, where it begins to rise again. A second peak is reached, followed by another decline; this process being repeated (fig. 20). The highest point occurs at the beginning of the experiment and the lowest shortly thereafter. From then on other peaks and low points occur, but none as high or as low as the first. This peculiar action can perhaps be explained by the molting characters of the animals. At the beginning all the individuals are more or less in the same phase, which may be termed a premolting, or intermolting, phase during which they feed heavily. Since the length of time between molts for different individuals varies greatly (p. 85), this difference in molting soon puts them out of step. This may explain why the highest and lowest points are found near the beginning because, after this time, all the individuals are not in the same phases at the same time. At very low temperatures the feeding does not occur as above described, but may be plotted in almost a straight line.

Figure 20 shows the number of milligrams of lettuce eaten per milligram of garden centipede at 28° C. No correction factor has been ap-

plied to the curve. It seems sufficient to state here that the average loss of weight for 50 check pieces of lettuce was 7½ per cent. An experiment at 18° to 20° C would probably show a better curve, since the correction factor subtracted for natural loss of weight of the lettuce would be less. The results of tests run at 18°, 20°, and 24° C are not included because

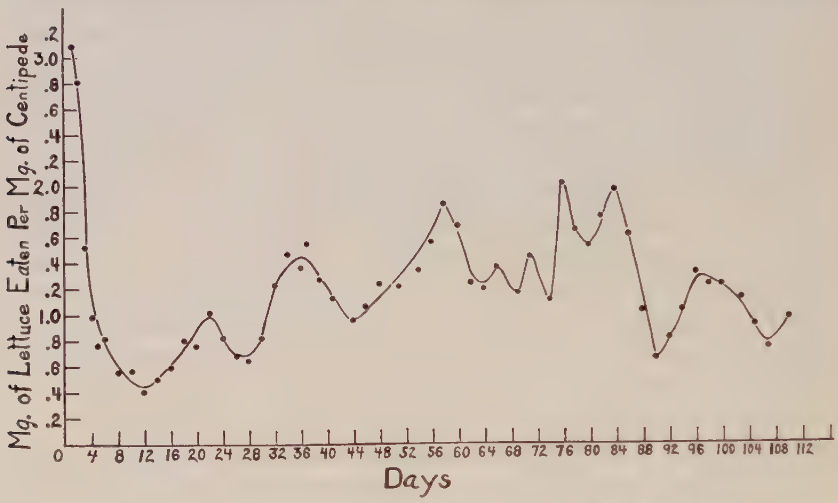

Fig. 20.—Feeding behavior of garden centipedes showing the milligrams of lettuce eaten per milligram of garden centipede at 28° C. Individuals used were obtained from lettuce leaves in storage cultures and were considered to be in the feeding phase. Note the heavy feeding at the beginning, and the low point which follows about 12 days later. A better feeding chart would be one in which the garden centipedes were held at lower temperatures.

the temperature varied so much after the first two weeks that it did not seem worth while to include them. They were comparable with that shown in figure 20. If further work is done, lower temperatures will be used, for 28° C is undoubtedly considerably higher than the optimum.

DESTRUCTIVENESS

Woodworth (1905*a*, 1905*b*) apparently was the first person to call attention to the damage to growing crops caused by the garden centipede. Davis (1912) observed it attacking young rootlets of fern asparagus (*Asparagus plumosus*) and smilax in a greenhouse in Illinois in 1908. Theobald (1912) also called attention to symphylans' damaging plants grown under glass in Guernsey.

Since this time, injury by the garden centipede has become more apparent, and at the present time the animal is a rather serious pest.

Numerous papers have been published in the United States which deal with this organism as an economic problem. Some of the more im-

portant of these are: Essig (1915, 1926); Compton (1930); Filinger (1928, 1931*a*); Herrick (1927); McDaniel (1931); Oregon Agricultural Experiment Station (1926): Riley (1928, 1929); Sheaffer (1930); Wymore (1924*a*, 1924*b*, 1931); and Michelbacher (1932*a*). Illingworth (1928*a*, 1929*b*) dealt with it as a pest in the Hawaiian Islands. The following discussed the economic significance of the garden centipede in foreign countries: in England, Walton (1930), Kearns and Walton (1932), Miles and Cohen (1935), and Speyer (1935); in France, Feytaud (1925, 1926), Larrieu (1934); in Portugal, Almeida (1930).

The garden centipede feeds on many different kinds of plants. The following list has been prepared to show, in part, its host range:

Alfalfa	Chrysanthemums	Mangels	Radishes, table*
Asparagus fern*	Colsus	Morning-glory	Radishes, wild
Asparagus, vegetable*	Corn*	Mushrooms	Rhubarb
Aster*	Cowpea	Muskmelons	Rose
Barley*	Cucumber	Mustard, wild	Smilax
Beans, common*	Easter lily	Needle grass	Snapdragons*
Bean, lima	Eggplant	Onions*	Spinach*
Beet, sugar*	Foxtail	Pansy*	Stevia
Beet, table*	Freesias	Parsley	Strawberry*
Calendulas	Gardenia*	Pea, garden*	Sugar cane
Calla lily	Geranium	Pea, sweet*	Thistle
Carnation*	Gladiolus	Pigweed*	Tomatoes*
Carrots*	Grasses*	Pineapple	Vetch
Cauliflower*	Lettuce*	Potatoes*	Wheat
Celery	Lettuce, wild*	Pumpkin	Zinnia*
Centaurea			

This list has been obtained from the literature and from observations made by the present writer. The number of plants shown probably represents only a small percentage of those actually attacked. For example, corn, barley, wheat, and foxtail grass are listed as host plants, and from these it can be assumed that all the small grains and probably many of the grasses would serve as food. Radish, cauliflower, and wild mustard are also attacked, which gives evidence that probably all other crucifers may serve as hosts. Thus, by using the present known host range, a greatly extended list can probably be deduced. Although in this investigation no serious attempt was made to determine the host range, the present writer feels confident that the pest will attack many other plants.

Many plants can withstand attacks of this pest; others, although susceptible to severe injury in the early stages of growth, are fairly resistant when once well established. For example, during the seedling stage of sugar beets, the garden centipede may completely destroy a germi-

* Hosts observed by present writer.

nating stand; yet, on the same soil, if the sugar beets can become established, they will grow to maturity and a crop can be harvested. Even such susceptible plants as snapdragons and sweet peas may do fairly well at times if they first have an opportunity to become established. Larrieu (1934) noted that corn plants which were 15 days old before being attacked were not appreciably damaged. But, even though such

Fig. 21.—An asparagus field that was heavily infested at time of planting. Bare spots indicate the large number of plants killed.

crops appear to be vigorous and healthy, the garden centipedes feed on them to some extent, and the yield is probably reduced somewhat. At present no methods for determining this loss have been worked out.

When seed is planted in heavily infested soil, the plants may never make their appearance above the ground. Under like conditions in greenhouses, young plants when set out may be so severely attacked that they make little or no growth. Such conditions may prevail and yet the grower will not be aware that the garden centipede is the offending organism. When plants are severely injured, they show a very noticeable lack of vigor. Injury is accomplished by eating the new roots or by eating the root as it leaves the germinating seed. In the case of larger roots small circular pits are produced by feeding.

In California, asparagus is one of the crops most severely attacked. Two types of injury are produced: The first is that caused when the asparagus is first planted in the fields. During this period the garden centipedes may attack the buds so severely as they begin to grow that they are unable to reach the surface. Injury of this nature (fig. 21) may prevent a satisfactory stand. Even in established fields where the fern growth might appear quite satisfactory, yields may be markedly reduced. The second kind of injury (fig. 22) is the small holes in the

growing spears made by the garden centipedes when eating, which show up as blemishes on the canned product.

Figure 23 shows the type of injury that occurs to young sweet-pea plants. In this case the garden centipedes have almost completely eaten

Fig. 22.—Garden-centipede injury to asparagus spears. Note the many feeding punctures in the spear to the left. (Photograph by E. O. Essig.)

away the roots. Figure 24 shows strawberry plants which have been attacked. The mother plant became established, but the roots of the daughter plants were eaten off as fast as growth took place.

The garden centipedes may also be indirectly responsible for losses. Because they feed heavily on the root system, they may open portals of entry for disease-producing organisms, as noted by McDaniel (1931), Illingworth (1928*a*), and Compton (1930). In several heavily infested areas in California, observations seem to support this belief, although definite experimental proof is lacking.

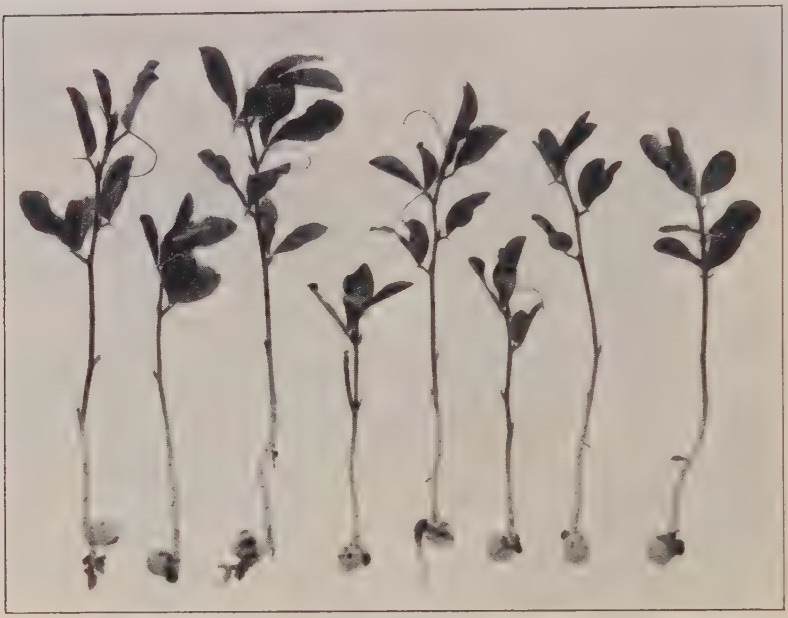

Fig. 23.—Sweet-pea seedlings injured by the garden centipede. In many cases the roots have been completely destroyed.

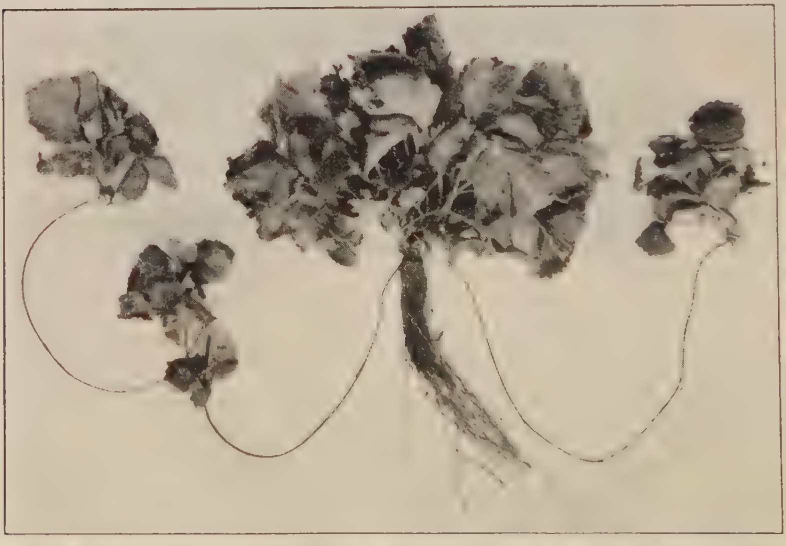

Fig. 24.—Strawberry plant from a heavily infested portion of a field. The daughter plants are rootless owing to the feeding of the garden centipede. The root system of the mother plant is also much smaller than that of normal plants of the same age.

CONTROL

The garden centipede has proved so destructive in numerous places that control measures have become necessary. In greenhouses it is best controlled by raising the benches so that there is an air space between the bed and the soil proper. This creates a condition which is not very favorable for the garden centipedes because their retreat into the subsoil is cut off. Despite this, under certain conditions, they may become so numerous as to cause serious injury. Then the soil must either be replaced or treated with steam or some fumigant. When ground beds are infested, proper steam treatment gives good control. Soil fumigants, such as paradichlorobenzene, calcium cyanide, carbon disulfide, and carbon disulfide emulsion, have also been used to good advantage. The present writer has

Fig. 25.—Flooding for control of the garden centipede in the Sacramento River Delta. (From Bul. 518.)

used paradichlorobenzene, carbon disulfide, and carbon disulfide emulsion with varying degrees of success. Some of the more important results, together with a fairly comprehensive review of the literature pertaining to control, have already been published (Michelbacher, 1932*a*).

Field control of this pest appears to be more difficult than that in greenhouses. Flooding the infested area for about two weeks or more is the most suitable and satisfactory method in California over the limited area where it can be carried out (fig. 25). This method of control is treated fully under the section on "Flooding." Here it is sufficient to say that Essig, Smith, and Gray (1918) were the first to suggest flooding as a control measure.

Poison baits have been used without any notable success. Partial control has been reported from Oregon (1930) where corn soaked in cor-

rosive sublimate was planted near each infested row. Thomas (1928), working in Pennsylvania, reported poison baits as nonattractive.

The present writer has done considerable work with poison baits. All studies so far have been carried out only in the laboratory. A large number of poisons were used, applied to either cubed carrots or red beets. It was found that most of the poisons were nonattractive and were avoided by the garden centipede. Sodium arsenite was the most effective, but even this seemed to be slightly repellent. In several experiments a perfect kill resulted; in others the kill varied between 60 and 100 per cent. This work was carried out before it was known that the garden centipede had feeding and nonfeeding phases. No doubt this would account for the variations that occurred. It is believed that if they were in the feeding stage, a 100 per cent kill would probably always result, and that the percentage killed would show a definite relation to the number of organisms in the feeding stage.

Many workers are of the opinion that frequent cultivation is unfavorable to the garden centipedes, and undoubtedly it does discourage them to some extent. Sanitary practices are also strongly advised, and care should be exercised to prevent the introduction of garden centipedes into noninfested areas. The manner in which this pest is probably most often spread (other than by its own locomotion) is by moving soil from one area to another. In moving potted plants, trays of plants, or balled plants, garden centipedes have undoubtedly been widely distributed. Such plants should never be transplanted into a noninfested area unless they are known to have been grown in soil free of the pest. Because the garden centipede is so widespread, there is difficulty in determining whether it occurred naturally in many areas or whether it was introduced. The answer to this might be found in comparing comprehensive surveys of regions with dense human populations with areas more recently put under cultivation and noting the frequency with which the pest is found. If it should be found much more frequently in the more populated areas, this might indicate that artificial dissemination is an important factor. So far, in any area that has been studied at all thoroughly, the pest has been found widely distributed.

BIOLOGICAL CONTROL

As early as 1851 Menge noted that the true centipedes were predaceous on the garden centipede. Filinger (1928, 1931*a*) reported that the garden centipede was attacked by at least two species and Wymore (1931) that it was attacked by four species of true centipedes. Very probably all species of the latter occurring in the same environment will attack

the garden centipede, and some of the smaller species may be of considerable importance in reducing the numbers of this pest. The present writer has often caged the two together and noted that the true centipedes attacked and ate the garden centipedes.

Wymore (1931) also reported a white, rapidly moving gamasid mite as attacking and injuring garden centipedes, both in the field and in

Fig. 26.—A garden centipede infested with hypopi, or migratory nymphs, of some species of tyroglyphids.

the laboratory. This mite was frequently found in abundance in the same habitat with the garden centipede, but so far the present writer has never seen it attack the latter. On several occasions the present writer has observed mites on garden centipedes, some of which were undoubtedly predaceous. In one case they were very numerous (fig. 26) and some specimens were sent to H. E. Ewing for determination. He reported them as hypopi, or migratory nymphs, of some species of Tyroglyphidae, probably *Tyroglyphus*. He stated that they were only riders and may be present by the hundreds on a single carrier. Other stages of the same species may be predaceous on the carrier.

Illingworth (1927*a*, 1928*a*) stated that at least two kinds of beetles, both larvae and adults attacked the garden centipede. These were *Philonthus discoideus* Gravenhorst and a cucujid *Cryptomorpha desjardinis* Guer.

The study of the natural enemies of the garden centipede has been neglected. This field will no doubt yield much interesting data when thoroughly worked out. There is no question but that many predaceous organisms prey on the garden centipede, and surely it must also be subject to bacterial and fungus diseases.

FLOODING

Wymore (1924*a*, 1924*b*) demonstrated that winter flooding is an effective method of controlling the garden centipede. In 1931 he again summed up the facts concerning winter flooding and concluded that for this to be successful, "Levees for holding the water should be substantially constructed and so placed that all portions of the field may be covered to a depth of 1 foot or more for two to three weeks." All flooding so far conducted has been restricted to the delta lands of the Sacramento and San Joaquin rivers. Here there is an abundance of water, and the water table is within a few feet of the soil surface. These two factors, together with the fact that there are rather large areas of more or less level land, probably account for the effectiveness of this control measure.

The reactions of the garden centipedes under these conditions have not yet been wholly determined. Data at hand indicate that when water is turned into a field, the water table begins to rise rather rapidly, so that some little distance away from where the water is being applied, the underground water reaches the soil surface at about the same time as does that which is flowing over the top of the soil. As the ground water begins to rise, there is a tendency for the garden centipedes to move up ahead of it. This results in the trapping of most of them in the surface soil. Conditions here are not favorable for their survival. This can perhaps be best accounted for by the fact that the structure of the surface soil is usually very loose, which allows it to become thoroughly saturated so that the only protection which the garden centipedes have is the film of air that may form about them.

Verhoeff (1933–34) observed that if trapped under water in a fissure, they might survive for a long time, and believed this was due to their ability to use the film of air which adhered to them. The protecting film of air seems to restrict their movements. Williams (1907*a*) stated that when submerged they wandered back and forth but rarely if ever broke through the surface film of water. In one experiment carried on by the present writer, in which infested plants were isolated by water, one garden centipede was observed walking around the bottom of the moat. It was able to make fair progress through the water, and as it walked along, its antennae were bent back somewhat, owing to the resistance offered by the water.

Several experiments by the present writer have shown that the movement of the garden centipedes into the surface soil during flooding is of large proportions. They congregate by hundreds if not by thousands in small clumps of soil which project above the surface of the water.

In such fields, disturbing the surface soil brought countless numbers to the top of the water.

On the other hand, all the garden centipedes do not reach the surface layer of soil. Some are trapped in air pockets, while others, in trying to move away from the rising water, work their way into blind cavities and thus find their avenues of escape cut off. Deeper in the soil, where its structure is firm and permeated by earthworm burrows and by countless fine cavities left by decaying roots, fairly large air pockets may be formed. Small air chambers may form in the tips of the finer cavities. These would give some protection to any garden centipedes that might be caught in them. In the experiments previously mentioned, it was also observed that, when all the garden centipedes in the surface soil appeared to be dead, live ones could be found in the deeper soil.

The kill obtained by flooding is probably determined, to a great extent, by the number of garden centipedes trapped deep in the soil. If most of them are confined to the surface soil, a good kill will result in a shorter time than when they are found deep. The conclusion, then, is that the high water table prevailing in the Delta of the Sacramento and San Joaquin rivers makes it ideal for flooding, and that the effectiveness of this method is due largely to the rising of the water table, which forces the garden centipedes to the surface. As yet no opportunity has been afforded to study flooding on land where the water table is located some distance from the surface. Whether flooding under such conditions is as effective as it is in the delta region would be an interesting point to determine. Possibly, the creeping of the water through the soil just ahead of the surface flow would have the same tendency to force the garden centipedes upward as does the rising water table.

Flooding as recommended by Wymore (1931) is not practical throughout the entire delta region. Among other objections, there are places where water cannot be raised to a height of a foot or more and be held there for two or three weeks because of excessive seepage. Where this occurs adjacent fields are soaked and road beds may be weakened or even flooded.

In such places it is believed that flooding during the warmer part of the year might be substituted for the winter method. One experiment along this line was conducted during May, 1934, at Clarksburg. Summer flooding probably has at least two advantages, both due to the higher temperature: first, the duration of flooding necessary to kill may be reduced; and second, probably only a very shallow depth of water is required to produce a satisfactory kill. In fact, it appears that the shallower the water the better the kill will be, for water of only a slight depth

warms up faster. When the temperature of the water is higher, the rate of metabolism is probably increased, fungi and bacteria become more active, and the garden centipedes are more rapidly destroyed. In the experiment conducted an 88.8 per cent kill was obtained after about 6 days of flooding. The percentage kill was based upon population studies made before and after flooding.

TABLE 6

TEMPERATURE CONDITIONS DURING EXPERIMENTAL FLOODING NEAR CLARKSBURG, 1934

Date	Air temperature,* °F		Temperature, °F, 6-inch soil level		Temperature, °F, 16-inch soil level		Position of recorder to flooding
	Maximum	Minimum	Maximum	Minimum	Maximum	Minimum	
April 29	78	49	65.0	60.5	65.5	64.0	
April 30	64	50	62.5	56.5	64.5	64.5	
May 2	77	46	64.0	59.5	63.5	62.5	
May 3	83	52	66.5	54.0	63.5	63.0	
May 4	88	56	86.5	55.0	75.0	61.0	Soil saturated
May 5	92	54	84.0	55.0	72.0	64.5	Soil saturated
May 6	83	56	68.0	57.0	71.5	68.5	Soil covered with ½–1 inch water
May 7	83	52	68.0	57.5	68.0	65.0	Soil covered with 1½ inch water
May 8	81	56	74.0	62.0	68.5	66.5	Soil covered with 1½ inch water
May 9	87	53	73.0	62.5	69.0	67.5	Soil covered with 1 inch water
May 10	97	60	73.0	65.0	69.5	68.5	Water at ground surface
May 11	98	54	76.0	65.5	69.5	69.0	Water off surface
May 12	91	59	73.0	62.0	70.0	69.0	
May 13	88	52	70.5	60.0	69.0	68.0	
May 14	91	53	70.5	60.0	69.0	68.0	
May 15	75	54	65.5	57.5	68.0	67.0	
May 16	76	50	65.5	57.5	67.0	66.0	

* Temperature for Sacramento, California, obtained from: United States Department of Agriculture. Weather Bureau Climatological Data, California Section.

The depth of water over the field in general was less than 6 inches and much of the area was submerged not more than 2 or 3 inches. Before flooding, the water table was at about 2 feet; a few days after the field was drained the water level stood at 22 inches. Table 6 has been prepared to show the temperature conditions which prevailed in the field before, during, and after it was submerged. Air temperatures as well as those for 6- and 16-inch soil levels are given. Data on flooding conditions are also included.

To show the contrast between temperatures that occur in winter and those that prevailed during the above experiment, table 7 has been included. Temperatures for the air and 6-inch soil level are given. The recorder was set up near Rio Vista where the soil was covered with 1

foot of water. The mean difference in maximum temperatures for the 6-inch soil level was about 23° F, while that of the minimum was only about 14° F. If the flooding were done in the summer or very early fall, a much greater difference might be expected.

During the May flooding, an examination of saturated soil almost at water level showed most of the garden centipedes to be dead. Where the soil was only slightly raised above the water level, conditions were such that many of them were able to survive. A glance at table 6 shows that the highest soil temperatures occurred just before submergence. This probably accounts for the kill at water level. After less than 24 hours of submergence, when the water was 1 or 2 inches deep, the disturbing of the surface soil brought many dead garden centipedes to the top of the water. Of 209 collected, 177 were dead. A special effort was made to collect those which appeared to be alive, so that the true ratio of dead to living was probably greater than that indicated. Two days later another examination of the same type was made and of 78 gathered only 1 was alive. Still a third examination around the edge of the field, shortly after it was covered, produced 1 live garden centipede out of 105 collected. In all cases garden centipedes could be brought to the surface by the hundreds, but collecting them was made extremely difficult because of the wind action. When examinations were made in the deeper soil, live garden centipedes were observed. Possibly if the temperature had been slightly higher, many of these would have been killed. Some evidence to support this was obtained in a laboratory experiment. At approximately 21° C, with a depth of water of 3½ inches, garden centipedes trapped in air pockets formed between the side of the container and the soil died in about 5 days, although at first they appeared to have sufficient protection to live for an indefinite period.

TABLE 7

Temperature Conditions during Winter Flooding near Rio Vista, 1933

Date	Air temperatures, °F		Temperature, °F, 6-inch soil level		Weather conditions
	Maximum	Minimum	Maximum	Minimum	
Dec. 14	55.0	41.0	51.0	49.5	Rain; south wind
Dec. 15	53.5	33.0	49.5	46.0	Cloudy; west wind
Dec. 16	51.0	31.5	47.0	45.0	Clear, cold; west wind
Dec. 17	46.5	36.5	47.0	45.0	Cloudy, cold; north wind
Dec. 18	54.0	37.0	46.0	45.5	Cloudy; east wind
Dec. 19	56.0	38.5	48.5	47.5	Clear; light north wind
Dec. 20	47.0	40.5	48.5	47.5	Foggy; light north wind

Shortly after the field was drained, no living garden centipedes could be found in the surface soil. In a few days, however, some of the survivors moved up. This is shown in the population study made after flooding (see table 9). Some symphylans were found to be more resistant to flooding than others. Besides the garden centipede, many of a species of *Symphylella* sp. were present. These survived flooding much better than the garden centipede, *Scutigerella immaculata*. They are much less active than the garden centipede, and no doubt they did not tend to move up ahead of the rising water table to the same degree as the latter. At least, in disturbing the deeper soil, they were found to be more abundant.

While flooding during the warmer part of the year shows much promise, it has some disadvantages. Most important of these is that it comes at a time when land should normally be in crops. This precludes its use where perennials are being grown.

POPULATIONS

Newport (1845) stated that a moist, light leaf mold at the roots of grass is the soil preferred by the garden centipede. Menge (1851) noted them in gardens and less often in woods in leaf mold under bushes and plants. He often had to look for hours to secure a single specimen. This is in marked contrast to many localities in this state where they occur in countless numbers. Muhr (1881) collected them in soil rich in humus, while Joseph (1882) obtained them in the soil under bat dejections in the Cave of Gurk. Grassi (1886) stated that *Scolopendrella* preferred stony places that were shaded, and believed that in general they were absent in the open cultivated country. Evans (1909), on two occasions, found the garden centipede, *Scutigerella immaculata*, occurring in ants' nests under stones. Williams (1907*a*) remarked that the chief factors determining its distribution seemed to be an atmosphere of great humidity, a moderate temperature, comparative darkness, and an undisturbed, or at least, an uncultivated, soil. Friedel (1928) concluded that the most important ecological factor for the spread of *Scutigerella* was moisture, not only the water content of the soil, but also the vapor content of air in the soil.

It is now known that the garden centipedes can be found under a wide variety of conditions, and they may apparently do about as well in a cultivated soil as in one left undisturbed. While the disturbance of the surface soil may interrupt their activity somewhat, and kill some, it has little effect upon them because their life is well adapted to subsoil conditions. This fact has been overlooked by many workers, who mainly confined their activities to looking under leaf mold, stones, etc.

In parts of the United States, France, Portugal, England, Hawaiian Islands, and probably other regions, they may be very abundant in farming areas and do considerable injury to growing crops. In a cultivated district, areas of heavy infestation do not seem to be large but are more or less localized in certain places. Figure 27 shows a portion of a cultivated field in which the garden centipede has caused serious damage.

Fig. 27.—A sugar-beet field heavily infested with garden centipede. Note the unevenness of the stand.

FACTORS INFLUENCING POPULATIONS

Populations of soil-inhabiting organisms are often difficult to ascertain. Even though numerous, they are easily overlooked. This is particularly true of those animals which spend their entire life within the soil. Because of its small size, the garden centipede is often unobserved; yet it may be plentiful enough to do serious damage. There are numerous factors which influence the distribution and population density of this organism. Among the more important are: location, vegetation, character of soil, moisture, and natural enemies.

Vegetation.—Vegetation has a marked influence on the distribution of the garden centipedes. An abundance of food probably stimulates breeding, and growing plants have the tendency to attract them to the surface soil, as shown in table 10 (p. 132), which represents a population study of a heavily infested greenhouse. Such attraction takes place particularly if the top soil is moist.

Soil Structure.—Soil structure has a very important relation to garden-centipede distribution. They seem to seek out those areas where the soil structure is more or less open. In such spots they are likely to occur in large numbers, whereas in compact soil they may be relatively scarce. The foregoing applies largely to the surface soil since the subsoil is

usually of much the same character over a given field. In the delta region of the Sacramento and San Joaquin rivers the subsoil is compact but so permeated by fissures left by decaying roots, earthworm burrows, and similar openings, that it affords ideal living conditions. In fact, in cultivated fields the subsoil furnishes a most favorable retreat for the garden centipedes. Except for winter and early spring, egg laying and most of their other activities appear to take place there. Of course, they can and do move into the surface soil, but that the deeper soil greatly favors them is evidenced by the tremendous number of molted skins found therein.

Injury to crops by this animal is usually most severe where the surface soil is loose. In one field where the garden centipede was doing considerable injury to a germination stand of sugar beets it was noted that a perfect stand was obtained in those rows that had been passed over by a tractor or a wheel of some other farm implement. Yet on either side of such a row serious injury occurred in places. In another field where the garden-centipede population was high, the farmer packed the surface soil and a fair stand of sugar beets was obtained. In all probability, the firming of the soil was partly responsible for this. The value of compacting the soil lies in the fact that the garden centipede is unable to make its own burrows. The animals are dependent upon cavities left by other soil-inhabiting organisms, decaying roots, and any other openings. Where the structure of the soil is loose, they may possibly have the ability to clear out passages to some extent.

In one heavily infested area under observation it was noted that as the season grew cold, large numbers seemed to seek the more open, loose soil. It appeared that vegetation had little attraction for them, and they were found more abundant in the open, porous soil than about growing plants.

Soil Texture.—Soil structure is largely determined by soil texture, so the latter is of considerable importance. Heavy-textured soils apparently are more favorable to the garden centipede than the light-textured soils, because of the greater permanency of the channels produced by decaying rootlets and worm and insect burrows.

Soil Moisture and Soil Temperature.—The garden centipedes react to the moisture supply in the soil in a very marked manner. They are not confined to any one soil level but have the ability to move up and down with the soil moisture and have been found ranging from the surface down to 4½ feet. Those found at 4½ feet were collected on January 1. They may possibly penetrate even deeper than this. The depth to which they may go is dependent upon soil structure as well as upon soil

moisture. In a single case where the top soil was moist and foliage was dense and lying close to the ground, garden centipedes were observed on the surface. Riley (1929) made similar observations. They have also been taken under boards after rains. In winter and early spring they are likely to be found rather close to the surface and may be collected within ¼ inch of the top of the soil. Later, as the earth begins to dry, they move deeper into it.

A number of investigators have noted that the garden centipede migrates 3 to 5 feet into the subsoil. Most writers report them in the deeper soil during the summer. Riley (1929), Compton (1930), McDaniel (1931), and Kearns and Walton (1932) called attention to this or similar migrations. Filinger (1931*a*) stated that they move downwards with the approach of warm weather in the spring. He gave the optimum temperature as 65° F. When the temperature of the soil at the surface reached 70° to 75° F. he claimed that the garden centipedes followed their runways to the subsoil 24 to 36 inches below the surface.

Miles and Cohen (1935) reported the optimum temperature for garden-centipede activity to be 50° to 60° F. They stated that as the temperature rises above this point, the animals migrate into the deeper, cooler soil. They believed that this preference for cooler conditions probably explains why injury to crops under glass is confined to the winter months. When seedlings were planted out, however, the garden centipedes, they found, would concentrate in the top 3 inches of soil, even though the surface temperature was slightly above what they considered the optimum.

Most of the work done by the above investigators was in greenhouses. Here in California the present writer knows of no such marked migration. As already stated, the most important factor seems to be moisture. In the San Francisco Bay area the present writer has found the garden centipedes very abundant in the surface soil during most of the summer where crops are being grown. In the warmer parts of the state, probably owing to irrigation, they have been observed close to the surface, even during the hottest weather. The present writer is inclined to believe that in the coldest weather they may move into the deeper soil to obtain more warmth, while during the summer a similar migration may take place because the deeper soil offers a cooler environment. Beyond a doubt, the garden centipedes have some definite temperature reactions, and a better understanding of them will be most valuable in directing control measures against this destructive organism. If the movements of the garden centipedes were only influenced by moisture and temperature, it would be a rather easy matter to study them, but an investigation of

these reactions is complicated by other influences such as food and soil texture and structure. These other factors have an important bearing as is evidenced by the fact that during the winter the garden centipedes have been found deep in the subsoil even though conditions in the surface soil appeared favorable for them as far as moisture and temperature were concerned.

Effects of Manure.—In places, farmers are reluctant to manure their land because they believe it may cause the garden centipedes to become so numerous as to do serious damage. Morris (1922*b*, 1927), in his population studies, showed that manure does increase the garden-centipede population, and the ratio of increase (1922*b*) is equivalent to 64 to 19. Davis (1924), Almeida (1930), Filinger (1931*a*), Feytaud (1926), and Larrieu (1934) also noted that heavy applications of manure made conditions more favorable for the garden centipede.

Gossard (1925) reported that some growers thought damage was reduced by using plenty of well-rotted barnyard manure, because they believed this to be the natural food of the pest which it would prefer to growing crops. This might possibly be the case, but from the results of this study, it appears that the garden centipede probably prefers succulent food and not manure, as believed by the growers.

There are places where manure has been used in infested regions without serious injury resulting. Experiments should be conducted to determine the full effect of manure on populations. Several investigators have reported a rise in soil populations after the application of manure. It certainly has more effect than just causing the soil to be more porous. For instance, manure has the tendency to stimulate plant growth, and an increase in succulent root growth might increase garden-centipede activity. The reproduction rate might be increased, and this would probably result in a marked rise in numbers. Also other factors must be considered. The manure may stimulate fungus and yeast growth, and these in turn may form an unlimited supply of food for the garden centipede. The effect of this type of food upon reproduction and increase is not known. Possibly such food serves the needs of the garden centipede as well as succulent plant growth. Under the heading "Food Habits," the garden centipedes were shown to feed readily upon yeast and perhaps upon other lower forms of plant life.

METHODS OF STUDYING POPULATIONS

From the previous discussion it is evident that there are many factors which affect the garden centipede, and that these tend to cause unequal distribution of the animal in a field. This heterogeneous occurrence makes it difficult to determine populations. Two other obstacles also

stand in the way of making accurate counts. It is necessary to develop, first, a satisfactory method of taking samples, and, second, a convenient procedure for separating the garden centipedes from the soil. Numerous ways of obtaining soil samples have been devised. The implement (fig.

A *B*

Fig. 28.—*A*, Instrument used in obtaining soil samples; *B*, modified Berlese funnel as developed by L. D. Christenson.

28, *A*) used in this study consists of a cylinder made of heavy galvanized iron 10 inches long and 4 inches in diameter, having a cross-sectional area of approximately one-half millionth of an acre. The bottom edge is beveled, and there is ½-inch slit running up one side to within 1 inch of the top which facilitates the removal of the soil. This instrument proved to be very satisfactory in moist soils which were not too compact and were free from rocks. Not all methods recommended for separating organisms from the soil are applicable to the garden centipede. Such a method as described by Morris (1922*a*), which depends upon washing the sample through a series of graduated screens, is not entirely suitable because the garden centipedes are so fragile that they are likely to become lost during the washing process. Modifications of this method, as used by Thompson (1924) and Edwards (1929), appear to have given satisfactory results. Separators which are patterned after a Berlese funnel (Berlese, 1905) are fairly satisfactory. An apparatus of this nature made by Christenson[13] at the University of California, in which

[13] Christenson, L. D. A Berlese funnel for collecting smaller soil animals. U. S. Dept. Agr. Bur. Ent. and Plant Quarantine. 5 p. May, 1936. (Mimeo.)

a light globe is used instead of a water jacket, is shown in figure 28, *B*. It is so constructed that the heat of a 100-watt lamp placed over the soil tends to drive the active organisms downward, whence they drop into the funnel and are collected in a bottle of alcohol placed at the outlet. Trägårdh (1933) successfully used a device similar to that developed by Tullgren (1917), which is very much like the one just described. He showed that under some conditions electric lights of different wattage, or even room temperature, should be used for best results according to the type of organism studied.

These devices which depend upon the free movement of animals, while highly desirable in the study of general soil populations, are of doubtful value in the case of the garden centipede. Since garden centipedes are easily killed or injured in handling the sample, many of them are not recovered. In the population studies of this organism, the method most used consisted in placing a sample 4 inches in diameter and either 6 or 9 inches deep into moisture dishes (9 inches in diameter). When the sample was 9 inches deep, it was divided into two parts. The soil was evenly spread out and all the larger pieces broken up. After this, water was slowly added through a funnel. The delivery end of the funnel was extended to the bottom of the dish, and, as the water rose, there was a tendency for the garden centipedes to move up. A few of them usually reached the surface of the soil and were carried on the surface by the water as it enveloped the soil. The floating individuals were easily removed with a dissecting needle, after which the soil was slightly stirred with the needle which usually brought additional specimens to the surface. Many of those coming to the top of the water were enveloped in an air bubble which remained just beneath the surface film of water. At first these were rather difficult to detect, but after some experience they were easily recognized. The soil was further agitated and more garden centipedes collected as they appeared. Later, stirring was done with a stick. With vigorous stirring some of them came to the surface in a wet condition, while others were mutilated, and both were difficult to recognize. Owing to the agitation, foam was almost certain to form on the surface, and the entangled animals were liberated by blowing on it. This flooding method has some advantages over others in that garden centipedes can be obtained which have been killed or injured in the taking and handling of samples, although not all of them in a sample can be extracted by such ordinary methods. Ten samples of one type of soil studied were each populated with a given number of individuals, and the average recovery was 66 per cent. The recovery from any one sample varied but slightly from this figure.

In taking field samples, it is not always easy to select locations that are representative of the area to be studied. The garden centipedes are seldom evenly distributed, and, if only 1 or 2 samples are taken, it is doubtful whether an accurate picture of the population can be obtained. In order to secure a fair average, at least 10 to 12 samples have been taken, which seems to give a rather complete idea of the numbers present. In the following discussion of populations, only the actual numbers collected will be dealt with, for they are all proportionally the same, and nothing would be gained by trying to reach a hypothetical total.

POPULATIONS STUDIED

A survey of the literature reveals that population studies of the garden centipede have not been treated to any great extent. An investigation by Williams (1931), which involved *Scolopendrella neotropica* Hansen and *S. simplex* Hansen, showed that in growing cane samples these creatures averaged about 90 per surface foot as against 150 in a fallow series. This is equivalent in the first case to 3,920,400 per acre, while in the fallow ground the number per acre is 6,543,000. These populations are somewhat greater than that of *Symphylella* sp. (2,705,000), found in the field studied by the present writer, but is far less than the garden-centipede, *Scutigerella immaculata*, population. Williams also noted that over half of the symphylans occurred between 5 and 9 inches beneath the surface.

In Austria, Friedel (1928), although conducting no extensive population studies, reached the conclusion that 1 square meter of favorable forest soil should furnish 50 garden centipedes.

Symphylans have figured in other population studies of invertebrate soil faunas. They were encountered by Morris (1922*b*, 1927), Thompson (1924), Edwards (1929), and Sawa (1930). In none of these cases were they found in large numbers, and probably represent the normal occurrence, whereas the studies to be reported here are for areas known to be heavily infested. Their population studies were made in several environments which included pasture, grass, and arable lands. The fact that they were found in most of the studies gives added evidence that they are fairly well distributed in nature. Thompson (1924) stated that the Symphyla constituted 86 per cent of the total Myriapoda population.

The above workers found the garden centipede distributed deeper in the soil than most of the other organisms, and Edwards (1929) found them more abundant in arable land than in a pasture area of a similar soil type. Sawa (1930) obtained like results. He found that the ratio for arable land to grass land was 392 to 54. Thompson (1924) found the reverse to be true. In order to convey some idea of the abundance and

relation of Symphyla to other soil invertebrate groups, a graph taken from Edwards (1929) is shown in figure 29.

In the present study two types of populations are considered: one from a field in the delta region, and the other from an infested greenhouse. Both were made during May and the first part of June, 1934.

Field Studies.—The field selected has been known to be infested for a number of years and the soil is well suited to the garden centipede. The surface soil to the depth of 9 or 10 inches is a brown silty clay, finely

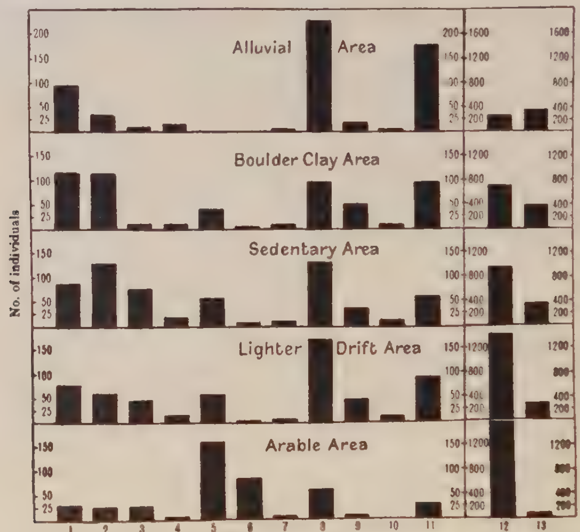

Fig. 29.—Relative frequency and occurrence of individual groups found by Edwards (1929) in his population studies. Note that the symphylans are most abundant in the arable area. *1*, Terricola; *2*, Terricolae cocoons; *3*, Nematoda; *4*, Gastropoda; *5*, Symphyla; *6*, Myriapoda other than Symphyla; *7*, Araneida; *8*, Acarina; *9*, Coleoptera; *10*, Rhynchota; *11*, Diptera; *12*, Collembola; *13*, Limicolae. (Reproduced by permission from the *Annals of Applied Biology.*)

granular in structure, with a high content of organic matter. The subsoil is a light gray silty clay, permeated with numerous fine cavities which serve admirably as runways for the garden centipede. During the spring of 1933 some damage was done to sugar beets growing therein, which necessitated two plantings, the second of which was also seriously injured. However, a satisfactory tonnage was harvested. In the late winter and early spring of 1934 the field was twice seeded to onions, and in each instance the garden centipede played a part in preventing a satisfactory stand. By May only a few seedling onions could be found, and the only other vegetation to be observed was a scattering of pigweed.

TABLE 8

RESULTS OF SYMPHYLAN POPULATION STUDY CONDUCTED BEFORE FLOODING IN A FIELD LOCATED IN THE DELTA OF THE SACRAMENTO RIVER

Sample* No.	Location	Depth in inches	Number of symphylans per square foot†		Number of symphylans per acre‡ in thousands (i.e., 000 omitted)	
			Garden centipedes	*Symphylella* sp.	Garden centipedes	*Symphylella* sp.
1	Weed spot	0–9	687	148	30,000	6,500
		9–18	103	57	4,500	2,500
		0–18	790	205	34,500	9,000
2	Free of vegetation	0–9	114	0	5,000	0
		9–18	172	68	7,500	3,000
		0–18	286	68	12,500	3,000
3	Weed spot	0–9	447	0	19,500	0
		9–18	57	57	2,500	2,500
		0–18	504	57	22,000	2,500
4	Free of vegetation	0–9	34	0	1,500	0
		9–18	297	11	13,000	500
		0–18	331	11	14,500	500
5	Weed spot	0–9	389	0	17,000	0
		9–18	687	68	30,000	3,000
		0–18	1,076	68	47,000	3,000
6	Free of vegetation	0–9	275	11	12,000	500
		9–18	183	0	8,000	0
		0–18	458	11	20,000	500
7	Weed spot	0–9	229	0	10,000	0
		9–18	91	0	4,000	0
		0–18	320	0	14,000	0
8	Free of vegetation	0–9	68	0	3,000	0
		9–18	57	0	2,500	0
		0–18	125	0	5,500	0
9	Weed spot	0–9	172	0	7,500	0
		9–18	744	22	32,500	1,000
		0–18	916	22	40,000	1,000
10	Free of vegetation	0–9	57	0	2,500	0
		9–18	217	0	9,500	0
		0–18	274	0	12,000	0
11	Weed spot	0–9	492	22	21,500	1,000
		9–18	45	22	2,000	1,000
		0–18	537	44	23,500	2,000
12	Free of vegetation	0–9	355	0	15,500	0
		9–18	263	252	11,500	11,000
		0–18	618	252	27,000	11,000
Average for the 12 samples		0–9	277	15.1	12,083	667
		9–18	243	46.4	10,625	2,042
		0–18	520	61.5	22,708	2,708
Average for weed spots		0–9	403	28.3	17,583	1,250
		9–18	288	37.6	12,583	1,667
		0–18	690	66.0	30,167	2,917
Average for spots free of vegetation		0–9	150	1.8	6,583	83
		9–18	198	55.2	8,667	2,417
		0–18	348	57.0	15,250	2,500

* Size of sample approximately 0.000002 acre.

† Calculated from sample (× 11.46).

‡ Calculated from sample (× 500,000).

This field was chosen for population studies for two reasons: First, it would give evidence of the number of garden centipedes present where serious damage to crops was being done; and second, it was to be flooded, and the effectiveness of such treatment could be determined at the same time. An examination showed most, if not all, of the garden centipedes to be in the first 18 inches of soil. The soil below this level was very wet, since the water table stood at about 2 feet. Because of the scattered vegetation, the pest was very unequally distributed. In taking samples, every other one was chosen so that it included the root system of a small weed. The other samples were obtained at least 2 feet away from growing plants. All the samples were taken in two parts, that is, 0 to 9 inches, and 9 to 18 inches. The results of this study are shown in table 8. The number of garden centipedes obtained from the samples range from 125 to 1,076 per square foot, the average being approximately 520, which is equivalent to about 22,708,000 to the acre. The average number obtained per square foot from samples taken near vegetation was 690, which is twice as many as obtained in the clear (348). Also, it is worth noting that where vegetation was growing, more garden centipedes on the average were taken in the first 9 inches than in the second 9 inches, while in the clear, slightly more were found in the second 9 inches than in the first. It was also observed that most of the garden centipedes were mature. Of all fields studied this one was the most heavily infested.

In the field examined a second symphylan, *Symphylella* sp., was present in considerable numbers so the data obtained concerning these are also shown in the table. The members of this species appear to be more unevenly distributed than those of the garden centipede and seem to prefer the deeper soil. On the average, three times as many were taken in the second 9 inches as in the first.

Table 9 shows the results of the population study after flooding. It shows that there was a great reduction in the number of garden centipedes. The average number recovered per square foot was 57.9 as compared with 520 before the field was flooded. Note also that *Symphylella* sp. withstood flooding especially well; there were 61.5 per square foot before treatment and 31.1 per square foot after treatment. Most of these that survived were found in the second 9 inches of soil.

Greenhouse Studies.—In the greenhouse chosen, the garden centipedes were very abundant, and the infestation appeared to be very uniform. The house was planted to snapdragons and all of them were affected to about the same extent. The plants had first been grown in small pots and were set out in ground beds about 2 months before the present writer had an opportunity to observe them. The only roots that

TABLE 9

RESULTS OF SYMPHYLAN POPULATION STUDY CONDUCTED AFTER FLOODING IN A FIELD LOCATED IN THE DELTA OF THE SACRAMENTO RIVER

Sample* No.	Location	Depth in inches	Number of symphylans per square foot†		Number of symphylans per acre‡ in thousands (i.e., 000 omitted)	
			Garden centipedes	*Symphylella* sp.	Garden centipedes	*Symphylella* sp.
1	Weed Spot	0–9 9–18 0–18	0.0 22.9 22.9	0.0 91.0 91.0	0 1,000 1,000	0 4,000 4,000
2	Free of vegetation	0–9 9–18 0–18	0.0 34.0 34.0	0.0 11.0 11.0	0 1,500 1,500	0 500 500
3	Weed spot	0–9 9–18 0–18	0.0 22.9 22.9	0.0 11 0 11.0	0 1,000 1,000	0 500 500
4	Free of vegetation	0–9 9–18 0–18	11.0 34.0 45.0	0.0 11.0 11.0	500 1,500 2,000	0 500 500
5	Weed spot	0–9 9–18 0–18	91.6 91.6 183.2	11.0 11.0 22.0	4,000 4,000 8,000	500 500 1,000
6	Free of vegetation	0–9 9–18 0–18	34.0 11.0 45.0	0.0 11.0 11.0	1,500 500 2,000	0 500 500
7	Weed spot	0–9 9–18 0–18	11.0 11.0 22.0	0.0 22.9 22.9	500 500 1,000	0 1,000 1,000
8	Free of vegetation	0–9 9–18 0–18	22.9 45.8 68.7	0.0 11.0 11.0	1,000 2,000 3,000	0 500 500
9	Weed spot	0–9 9–18 0–18	137.0 11.0 148.0	0.0 34.0 34.0	6,000 500 6,500	0 1,500 1,500
10	Free of vegetation	0–9 9–18 0–18	22.9 0.0 22.9	22.9 34.0 56.9	1,000 0 1,000	1,000 1,500 2,500
11	Weed spot	0–9 9–18 0–18	22.9 0.0 22.9	0.0 11.0 11.0	1,000 0 1,000	0 500 500
12	Free of vegetation	0–9 9–18 0–18	0.0 57.0 57.0	0.0 80.0 80.0	0 2,500 2,500	0 3,500 3,500
Average for the 12 samples		0–9 9–18 0–18	29.4 28.4 57.9	2.8 28.2 31.1	1,292 1,250 2,542	125 1,250 1,375
Average for weed spots		0–9 9–18 0–18	43.7 26.6 70.3	1.8 30.2 32.0	1,917 1,167 3,083	83 1,333 1,417
Average for spots free of vegetation		0–9 9–18 0–18	15.1 30.3 45.4	3.8 26.3 30.2	667 1,333 2,000	167 1,667 1,333

* Size of sample approximately 0.000002 acre.

† Calculated from sample (× 11.46).

‡ Calculated from sample (× 500,000).

they had were those which were contained in the more or less firm soil that surrounded the plants when they were removed from the pots and transplanted in the beds. Many of the pests penetrated into this soil

TABLE 10

RESULTS OF GARDEN-CENTIPEDE POPULATION STUDY CONDUCTED IN GREENHOUSE

Sample* No.	Location	Depth in inches	Number of garden centipedes per square foot†	Number of garden centipedes per acre‡ in thousands (i.e., 000 omitted)
1	Snapdragon root system	0–6	2,910	127,000
		6–12	515	22,500
		0–12	3,425	149,500
2	Interspace	0–6	160	7,000
		6–12	103	4,500
		0–12	263	11,500
3	Snapdragon root system	0–6	4,011	175,000
		6–12	687	30,000
		0–12	4,698	205,000
4	Interspace	0–6	206	9,000
		6–12	412	18,000
		0–12	618	27,000
5	Snapdragon root system	0–6	2,922	127,500
		6–12	504	22,000
		0–12	3,426	149,500
6	Interspace	0–6	275	12,000
		6–12	286	12,500
		0–12	561	24,500
7	Snapdragon root system	0–6	2,658	116,000
		6–12	664	29,000
		0–12	3,322	145,000
8	Interspace	0–6	275	12,000
		6–12	504	22,000
		0–12	779	34,000
9	Snapdragon root system	0–6	2,590	113,000
		6–12	493	21,500
		0–12	3,083	134,500
10	Interspace	0–6	229	10,000
		6–12	286	12,500
		0–12	515	22,500
Average for the ten samples		0–6	1,624	70,850
		6–12	445	19,450
		0–12	2,069	90,300
Average for snapdragon root systems		0–6	3,018	131,700
		6–12	573	25,000
		0–12	3,591	156,700
Average for interspaces		0–6	229	10,000
		6–12	318	13,900
		0–12	547	23,900

* Size of sample approximately 0.000002 acre.

† Calculated from sample (×11.46).

‡ Calculated from sample (× 500,000).

mass, but they were most abundant in the soil surrounding it. At planting time the soil was not firmed about the plants, and as a result there was an area of very loose open soil. This was literally swarming with the organism.

The plants were set out 8 inches apart each way. In order to obtain samples that would give the true population, every other sample included a plant. The other samples were taken in the center of the interspaces. Thus, one set of samples was taken at the point of highest infestation and the other at the lowest, so that the average of the two should give the correct population for the house. Samples were taken in two parts, at depths of 0 to 6 inches, and 6 to 12 inches. An examination showed that a few of the garden centipedes were deeper than 12 inches, but, since most were present in the surface soil, it was thought unnecessary to go beyond the 12-inch level. Garden centipedes encountered were of all sizes. The results of this study are shown in table 10. The average number recovered for each of the ten samples equaled 2,069 per square foot, which, if expressed as the number per acre, equals 90,300,000. The average for the samples which included the plants, if taken alone, is 3,591 per square foot, or 156,700,000 per acre, while those for the interspace equaled 547 per square foot, or 23,900,000 per acre. This population study clearly shows to what degree plants may attract this pest. From the samples taken about the plants, 3,018 garden centipedes per square foot were recovered on the average from the first 6 inches, and only 573 per square foot from the second 6 inches. For the samples taken in the interspaces, on the whole, more garden centipedes were taken from the second 6 inches than from the first. Table 10 clearly indicates that the samples of the same group agree rather closely with one another. This gives evidence of an even distribution of the pest throughout the house. These results are rather similar to those obtained in the field above described but are much more clear cut.

SUMMARY

The garden centipede, *Scutigerella immaculata* (Newp.), is a member of the family Scutigerellidae, the order Symphyla, and the class Symphyla, which is one of the four classes of Myriapoda and is more closely allied to the classes Diplopoda and Pauropoda than to the Chilopoda.

This animal is widely distributed in the Northern Hemisphere but is known to occur only in a single locality south of the equator. Other species of Symphyla are found widespread throughout the world; their northern distribution seems to be limited by expected minimum temperatures of about —15° F.

Methods of etherizing the garden centipede and the importance of proper illumination for making examinations are discussed.

A type of storage culture was developed in which the animals repro-

duced readily, and, when properly cared for, furnished a continuous and unfailing supply of individuals for experimental study.

The earliest that egg laying was observed to begin was between the seventh and eighth molts, which would indicate that this is about the time sexual maturity is reached. In most cases eggs were not obtained until a much later date. Oviposition occurs a short time before molting.

At birth the garden centipede has 6 pairs of legs and 6 antennal segments. There are 11 scuta unless the last one is considered to be made up of an anterior and posterior section, in which case there would be but 10. With the successive molts more segments are added to the antennae, the scuta are increased to 15, and the legs to 12 pairs. With the sixth molt the organism receives all its morphological parts, but complete differentiation does not occur until a much later period, the life history being very complex.

After each molt more segments are usually added to the antennae. This behavior has been observed in individuals nearly three years old. Broken antennae are regenerated.

The garden centipede molts from time to time during its entire life and since it may live for a period of four years or more, the maximum number of molts probably exceeds 50. The molting characteristics of different individuals vary greatly; a sex factor is known to be present, and some evidence has been obtained which indicates that a genetic factor may be involved. Other factors which influence molting are: type of food, temperature, humidity, and mutilation.

Temperature markedly influences molting, which is most frequent at 28°C. Above and below this point the molting rate decreases. A temperature of about 37°C is lethal. The organism can survive a temperature of 2°C for long periods, but seems unable to withstand 0°C for any length of time if previously held at room temperature. Garden centipedes first held at 4½°C may withstand a temperature of 0°C for months. The optimum temperature falls somewhere between 12° and 20°C.

With regard to certain external anatomical features, the present writer believes that there are 8 fully developed coxal sacs on the third to the tenth body segments, inclusive. There appear to be rudiments of such structures also on the second, eleventh, and twelfth segments.

Respiration is carried on by means of two cephalic stigmas and their connecting "tracheae." Many authorities also believe that the coxal sacs are respiratory in function.

The garden centipede appears to be a vegetable feeder and to prefer succulent materials, although it feeds on many kinds of lower plant life.

In certain areas the garden centipede is a serious pest to cultivated

crops. Under field conditions flooding is the most satisfactory method of controlling it. Suitable methods for checking damage in greenhouses consist in using raised benches, in steam treatment, or soil fumigation. True centipedes, or chilopods, are among the most important natural enemies.

The garden centipede is not restricted to any particular soil level. It may be found from the surface to a depth of 4 feet or more. Moisture seems to be the most important factor determining its vertical distribution. Other influencing factors are: temperature, soil texture, soil structure, and vegetation. Population studies in the field and greenhouses show that these animals may be present in large numbers, sometimes as many as 22 millions per acre out of doors, and 90 millions per acre under glass.

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